GAGE (Simon H.)

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LAKE AND BROOK LAMPREYS

OF NEW YORK

ESPECIALLY THOSE OF CAYUGA AND SENECA LAKES

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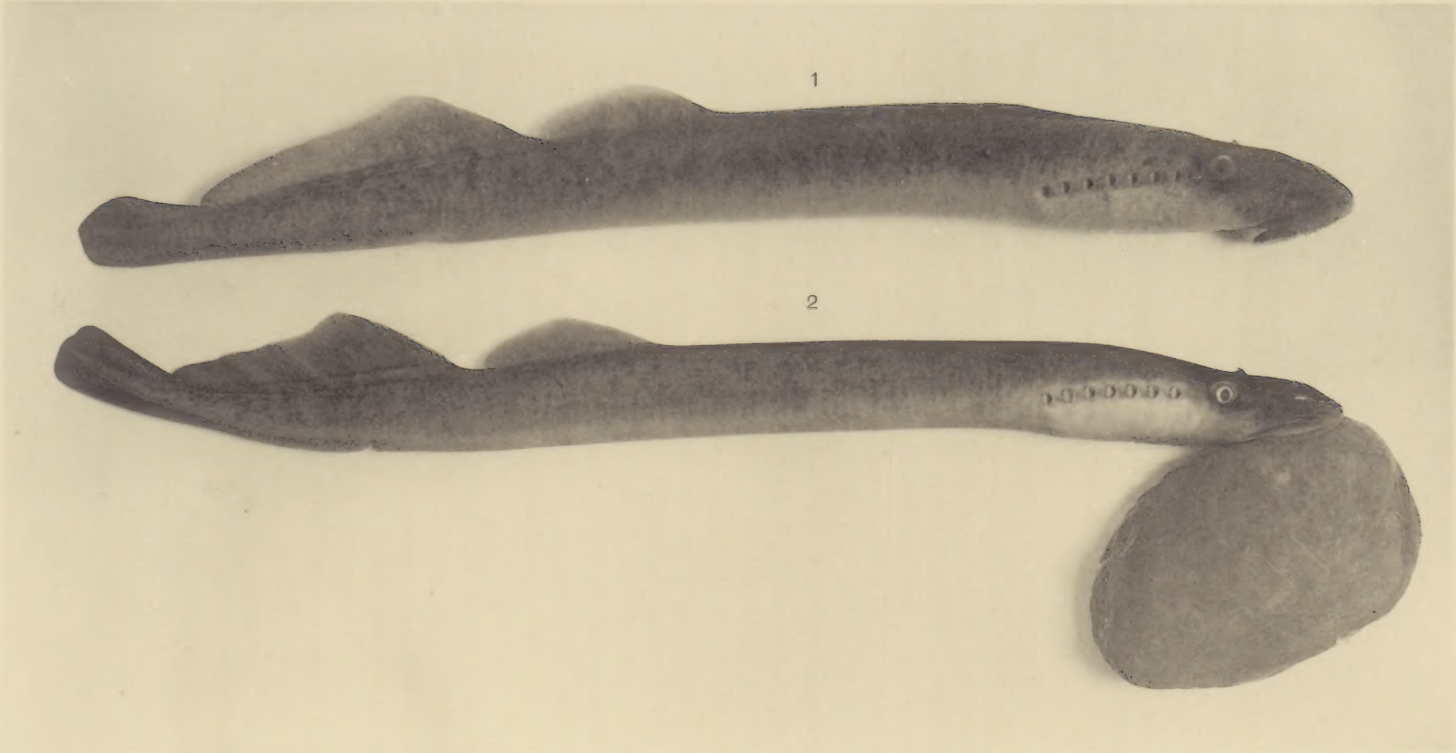

PAIR OF LAKE LAMPREYS FROM THE SAME NEST.

THE LAKE AND BROOK LAMPREYS OF NEW YORK, ESPECIALLY THOSE OF CAYUGA AND SENECA LAKES.

By SIMON HENRY GAGE.

If one glances at a topographical map of the State of New York, there will be seen in the western half a remarkable series of long narrow lakes, with a general north and south direction. These lakes occupy a basin between Lake Ontario on the north and a ridge that separates this basin from the Mohawk River on the south-east, and the Susquehanna River and its tributaries on the south. This elevation bordering the lake basin on the east, south and west, and forming nearly a semicircle, is drained to the north into the lakes, and into the Susquehanna and Mohawk Rivers on the south. The area of elevation draining into the Mohawk, and thence to the Hudson River is, however, comparatively slight.

The central and largest of these lakes is Cayuga (Pl. 2), flanked on the west by Seneca, next in size, then come Keuka, or Crooked, and Canandaigua Lakes. On the east are, in order, Owasco, Skaneateles, Onondaga and Oneida Lakes. In addition to these are numerous small lakes or ponds scattered among the large ones. A further study of the map will show that all of these lakes have important tributaries especially at the head. The outlet either flows into one of the larger lakes or directly into a common outlet. The final destination of all the superfluous water is Lake Ontario, through the Oswego River; and thence through the St. Lawrence River it reaches the Atlantic Ocean, 700 to 800 miles to the eastward. With the other great lakes the connection is by the Niagara River, the falls forming, at the present time, an impassible barrier against the passage of fishes from Lake Ontario to the other great lakes.

From these, the present connections, and from the possible connections with the Susquehanna and Hudson rivers at an earlier date, it is to be expected that the aquatic fauna of Cayuga and the other inland lakes would be rich and varied.

By assiduous personal study and observation and the wise direction of students, Professor Wilder has shown that in the Cayuga Lake basin there are 21 families, including 40 genera and 59 species representing the group of fishes.

A further study of the outlets of these lakes, to Lake Ontario and thence to the ocean, reveals the fact that they are long and tortuous, and besides possess many rapids and shallows. These conditions have probably obtained in recent geological time, a time sufficiently great to lead one to expect that the lake forms, especially those that had ceased to be migratory, would have received a certain stamp or impress from the special and somewhat isolated environment. Furthermore, migratory or anadromous forms, in bodies of water like these, where they are surrounded by plentiful food, might gradually become less migratory and as the difficulties of reaching the ocean were increased by changes in the character of the outlet or the gradual recession of the ocean, they might finally remain permanently in the fresh inland waters, and like the other permanent inhabitants be modified by the special environment.

The more this lake fauna is studied the clearer does the local coloring, so to speak, appear. Among the lampreys, the subject of this paper, there appears not only the local impress but almost positive evidence that forms, at one time naturally passing their adult life in the ocean, have become accustomed to remain permanently in fresh water with corresponding changes in the more impressionable or less important parts. I say more impressionable, for it is one of the fruits of modern research, in the light of evolution, that the most fundamental organic structures, having to do with the mere existence of an organism without regard to its upward progress, are more persistent and less changeable than less ancient and less important organs, that is, less important from the mere existence standpoint.

Problems having a philosophical bearing have always been the most fascinating to the natural philosopher as well as to the metaphysician. In the study of living organisms this has been especially true since the doctrine of evolution has so profoundly influenced thinking men. Naturally therefore, Professor Wilder, who came to his professorship in Cornell University—which itself was making a leap in educational evolution—during the time when evolution and various collateral hypotheses were in the fiercest conflict with all previous doctrines, theological and otherwise—naturally Professor Wilder turned with especial interest to the study of the Cayuga Lake fauna which promised information concerning the effect of local environment, and change from preceding conditions. Naturally also he turned with especial interest to the lamprey, the lowest representative of the vertebrates found in the lake fauna.

This interest was transmitted to his pupils, and since 1875 the writer of this article has lost no opportunity of studying the lampreys at all stages of life, and this study has been devoted to the living animals rather than to the dead organisms, although the understanding of their activities and physiological functions has been constantly clarified by experiment and anatomical study.

Characterized zoologically the lampreys (Petromyzontidæ) are fish like vertebrates, with an eel- or snake-like form and a metamorphosis, comparable to that of frogs and toads. The skeleton is wholly cartilaginous and the notochord persistent. Neither pectoral nor pelvic limbs nor their arches are present although the dorsal and caudal fins are well developed. The branchiæ are extended, and open by seven independent openings on each side, and in the adult the gills are pouched (whence the name Marsipobranchii sometimes used). The nasal sac is single and blind and opens to the exterior by a raised papilla on the dorsimeson just cephalad of the median, or pineal, eye and of the paired eyes. Apparently no jaws are present and the mouth in the adult is suctorial and armed with horny teeth; but the rudiments of jaws have been shown by Huxley and others to exist. The tongue is a piston-like rasp in the adult, absent or rudimentary in the larva.

According to all zoologists the lampreys (Petromyzontidæ) are very low in the zoological scale, and according to many they are degraded forms. They are found in the temperate regions of both the northern and southern hemispheres ; and all, so far as investigated, lay their eggs in fresh water and pass their larval life there. Some pass their entire life in fresh water while others go down to the sea, but all finally, on the attainment of sexual maturity, once more ascend the streams to their birth-place where the eggs for a new generation are deposited, thus completing the life cycle.

Both the lake and the brook lamprey agree entirely with the designation for the Petromyzontidae as given above, and besides the lake lamprey agrees with the characters given for the genus Petromyzon, viz. : The supraoral lamina, or maxillary tooth-plate, is contracted and with two cusps placed close together ; infraoral lamina or maxillary tooth-plate with six to nine cusps. The discal teeth are in concentric series ; those on each side of the mouth are bicuspid. (Pl VI).

With reference to the specific relationship of the large lake lamprey there has been considerable diversity of opinion. Up to the year 1875, the University had only secured small lampreys caught on fish, none of them exceeding 15 to 20 centimeters. The coloration of these lampreys was white on the ventral half and nearly uniformly black, or bluish black along the dorsal half of the body. In the spring of 1875, however, there was obtained from Cascadilla Creek, near the University, a specimen nearly twice as large as the ones usually obtained and with a strikingly different general appearance, due in part to the greater size and more variegated coloration, but mostly to a large rope-like ridge extending along the back from the gills to the dorsal fin. The two dorsal fins were continuous, simply having a depression between them. The specimen was photographed when fresh and is reproduced in Pl. III, fig. 5. The general appearance, so strikingly unlike either the small lake lampreys previously obtained or the specimens of true sea lampreys in the museum, seemed to indicate that, responding to its special lacustrine environment this lamprey had assumed characters which

might be considered generic or at least specific ; and Professor Wilder suggested to his special class, before which the specimen was brought for study and comparison, that if the peculiarities noted in this first specimen were found constant and characteristic of the lake lamprey one might consider it a distinct species at least and give it the specific designation of *Petromyzon dorsatus*, from the dorsal ridge. But believing that the admonition to "prove all things and hold fast that which is good" should be followed in science as well as in philosophy, publication was reserved until other specimens could be obtained to show whether the first was typical or a mere sport or transient variation from the truly typical form.

It fell to the writer, then student assistant to Professor Wilder, to prosecute the search for other examples of the lake lamprey and to aid in the final solution of its life history and systematic relationship, the work being constantly forwarded by the advice and encouragement of Professor Wilder, as well as by the freest use of his personal notes and drawings.

In prosecuting the investigation almost no aid was obtained from the lake fishermen. All they knew about the lampreys was that they were sometimes caught clinging to other fishes. One man, however, living near the inlet, brought to the laboratory six larvæ and stated how they were obtained. He also said that the large ones went up the inlet in the early spring. By diligent inquiry of people living near the inlet, information was obtained so that in the spring of 1876 the explorations of the inlet were successful and the adult ones were found spawning, and the larvæ were found in the sand banks along the edges of the stream. Of the seven large lake lampreys caught, five possessed the dorsal ridge so characteristic of the first one obtained. Upon dissection it was found that the ridged ones were males and those without the ridge females, so that from this time on it was exceedingly easy to determine the sexes in fresh specimens by this feature alone. Alcoholic specimens which had been caught in the breeding season were far less easily separated into the two sexes by this sign since the body was badly shrunken in alcohol, and the females so preserved often appeared to have nearly as large a ridge as the males. In

1878–1879 specimens were submitted to Prof. D. S. Jordan, who designated the lake lamprey as *Petromyzon nigricans* of Leseur in the synopsis of the fishes of North America ('82), remarking: "It is possibly only a variety of *P. marinus*."

During the college year, 1885–86, S. E. Meek, one of Professor Jordan's students, as fellow in zoology in Cornell University, made a special study of the fishes of the Cayuga Lake basin; and from the interest already aroused in the lampreys of the lake, he joined the writer, during the spring of 1886, in a critical and extended examination of the lake lampreys. Nearly 800 specimens were studied, especially as to external sexual characters and specific relationships. In a joint communication before the American Association for the Advancement of Science (Gage and Meek, '86) the following points were presented: (a), "The determination of the specific identity of the large Cayuga Lake lamprey and the sea lamprey; (b), The determination of the constant presence of a dorsal fold or ridge in the males and of a ventral fin-like fold in the females of [the Cayuga Lake] *Petromyzon marinus*, at the breeding season."

Jordan and Fordice ('85), in "a review of the North American species of Petromyzontidæ," remark concerning the Cayuga Lake lamprey. "We have examined marine examples of this species [*P. marinus*,] and also numerous specimens in all stages of growth from the larva to the adult form, collected by Dr. Burt G. Wilder, in Cayuga Lake, at Ithaca, N. Y. Among these are types of *Petromyzon dorsatus* Wilder, which seems to be merely a land-locked form, not permanently distinct from *P. marinus*. The characters assumed to distinguish this form from the true *marinus* are, however, more or less inconstant and not of specific value."

Even after the extended study of the 800 specimens mentioned above, there still remained to be settled the question whether or not the external sexual characters of the dorsal ridge in the male and the anal fin-like structure in the female were constant throughout the year or merely seasonal characters comparable to so many others known in the animal world. There was also the query whether the American,

true, anadromous sea lamprey developed the peculiarities found in the lake lampreys at the spawning season, and according to Seeley ('86) also present in the European marine lamprey during the breeding season.* Until these questions could be satisfactorily answered there would remain doubt as to the really constant peculiarities developed in the lake form. During the winters of 1875 and 1877 large lake lampreys were obtained of both sexes, and concerning them the notes either say "no ridge" or "ridge very low and broad," so that additional information must be sought. In the autumn and winter of 1886–87 great inducements were offered to the lake fishermen to obtain large lampreys. During that winter and since then throughout the year, large specimens were obtained and brought to the University. All of these large specimens looked alike. There was no dorsal ridge in any of them nor was there an anal fin or projecting urogenital papilla in any of them, and the two dorsals were well separated in all (Pl. III, fig. 6). It was only on dissection that the sexes could be distinguished. Thus it was definitely determined during the autumn and winter of 1886–87, that it was only during the spawning season that the special external sexual characters appeared in the lake lamprey.

In answer to the second query concerning like seasonal peculiarities in the true marine lamprey: alcoholic specimens obtained at various seasons were examined, but as stated above, whether or not a ridge was present during life is not easy to determine from alcoholic specimens. So that while ridges appeared on some of them, it was found by dissection that the animals were in some cases males, but quite as often females. Uncertainty must therefore continue until a considerable number of fresh specimens could be examined. This was made possible by the intelligent aid given by Mr. Thomas S. Holmes, of Lawrence, Mass., who sent specimens of the marine lamprey which were running up the Merrimac River to spawn. The specimens were usually sent in the early or middle part

* During the month of August, 1889, the writer saw in the aquarium of the Trocadaro in Paris several large marine lampreys, some of which possessed very prominent dorsal ridges.

of June, that is, in the height of the running season. Some males exhibited a ridge, but many none, so that it was not possible to distinguish the sexes with certainty by the external appearance.

In 1893 it was found that a fully mature lake lamprey obtained April 10, that is about fifty days before the time for spawning, showed none of the seasonal characters, and hence it seemed likely as the spawning grounds of the true marine lampreys were so far from the ocean, that some might set out on their journey to them before any special, external sexual characters appeared. To determine this, Mr. Holmes was asked to secure the first lampreys that should be found running up the Merrimac, and also some at the very close of the season. This was done during the present year (1893). Those caught about May 20, were found without either ridge or anal fin, and the sexes could not be distinguished by any external feature. On dissection, the sexual products were found to be still firmly imbedded in the ovary and testis, or spermary, and in many of them the alimentary canal was large, showing little or no signs of atrophy, except at the terminal part. On July 8, there were received four specimens. Only two were seen by Mr. Holmes after these were caught so that those sent were among the last to ascend the stream. These showed in an unmistakable manner the external characters so striking in the two sexes of the spawning lake lamprey, viz., a ridge extending from the gills to the dorsal fin in the male and an anal fin-like crest in the female. In both sexes the sexual products were partly shed into the abdominal cavity.

Information from the spawning grounds at the head waters the Merrimac River in New Hampshire, shows that the dorsal ridge has been noticed by those familiar with the lampreys in that region.

The dorsal fins in the male especially, are in some cases considerably approximated, but in only a few cases have the marine lampreys shown an appearance of continuity of the two dorsals.

It thus appears that the peculiarities so striking in the first

lake lamprey obtained, are present in the males only, and are seasonal and very temporary. Furthermore, in addition to the characters mentioned above as common to the sea and the lake lamprey, the determination that in the true marine lampreys similar sexual peculiarities occur at the breeding season, removes the last element of doubt as to the very close relationship of the lacustrine and marine forms.

With reference to the specific identity of the lake and the marine lamprey, it seems impossible to doubt that they were originally identical, and that the lake lamprey in its somewhat isolated, inland home has become considerably modified. The most salient and important modifications relate almost wholly to the adult form so far as is known ; for the larvæ of the sea lamprey from the Susquehanna River agree so closely with those of the lake that if several living or similarly preserved specimens of about the same size from each locality were mingled, it would be difficult or quite impossible to again separate them. This argument may not be of great importance, however, for as it will be shown later, no definite distinctions between the larvæ of the lake and of the brook lamprey have yet been discovered. The modifications in the adult form are : (a), A very much smaller size for the lake lamprey ; the average length in the breeding season being frequently less than half that of the sea lamprey. The dorsal ridge is relatively much more prominent in the male lake lamprey in the breeding season than is that of the sea lamprey, and the two dorsal fins are more nearly fused ; likewise the urogenital papilla of the male, the notched appearance at the vent and the anal, fin-like fold in the female are relatively greater in the lake than in the sea lamprey. There is more frequently a larger number (8 to 9,) cusps or teeth to the infra-oral lamina, or the mandibular tooth-plate, in the lake lamprey than in the sea lamprey ; and finally there is a greater development of cutaneous pigment and it is more diffusely arranged so that the general coloration of the lake lamprey seems more uniform, and on the whole somewhat darker than with the sea lamprey. Indeed, the marine lamprey is designated by the fishermen as the large spotted lamprey.

Whether these differences, which are mostly of degree, are sufficient to constitute two different species, has been decided in the negative by Jordan, and also by Meek ('82, '85, '88). If the criterion of natural and spontaneous interbreeding be taken to settle the question, it must receive a different answer ; for the lake lamprey, from its size alone would not form a mate to the marine lamprey. Of course they are not upon the same spawning grounds, but any one who has watched the spawning of lampreys, (see below under spawning) would, I feel sure, agree with me that the difference in size is so great that even if on the same spawning grounds, they would be mutually incompatible. It is not asserted that it would be impossible to fertilize the ova of a marine lamprey with the zoosperms of a lake lamprey and the reverse, but the criterion of modern systematists is, not possible inter-fertility under very artificial conditions or by the intervention of man, but the natural interbreeding under conditions to which both forms have been subjected for many generations.*

Now while I firmly believe that within comparatively recent times, geologically speaking, the lake lamprey was a true anadromous marine form it seems to me that at present, judged by the physiological test of interbreeding, it would be better to consider the lake lamprey a distinct species, and to designate it either as *Petromyzon unicolor* DeKay, or *P. dorsatus* Wilder, should the Lake Champlain larvæ, upon which

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* For possible readers of this article who have not followed closely the progress of views concerning classification and the nature of "*a species*," it may not be out of place to add that by biologists (this term including both morphologists and systematists) it is believed that "*species*" as an entity in nature, has no existence as was formerly taught, but that the arrangement of closely allied forms into groups or "*species*" is largely for convenience. And as some criterion must be used, the physiological one mentioned above seems to have gained the greatest favor.

As is shown in another article in this volume (J. H. Comstock's), while the practical aim of classification is to subserve convenience, its true purpose is to show the phylogenetic relationships of organisms, and the permanence of any system will depend directly upon the approximation with which this purpose is attained.

DeKay's name was based, prove to be the larvæ of the marine lamprey, which is probable (see Jordan and Fordice, '85, p. 284).

Distribution of the Lake Lamprey.—It is known by personal observation and collecting, to be abundantly present in Cayuga and in Seneca Lakes; and from information obtained concerning the other lakes and from Lake Ontario, it is believed to be present in them also. It is hoped that during the next five years all of these regions can be visited and all the lakes and watercourses of the State investigated to determine the presence of lampreys and their correlation with those now under consideration. It is hoped also to extend the investigation to the Great Lakes and to bring any lampreys there living into the field of comparative observation.

Comparison of the Sexes.—As stated above, except in the spawning season there are no definite external characters by which the sexes can be distinguished. The question then arises as to the necessary steps to make the determination, at any other time than in the spawning season. The only way, so far as is known to the writer, is to resort to dissection. This is the only way also for determining the sex in the larvæ. Upon dissection, even in larvæ 100 milimeters in length, the sexes may be quite readily distinguished by examining the gonads, as the ovary and the ova are markedly larger than the spermary and sperm mother-cells (Pl. VII, fig. 37, 38). The determination of the sexes in large, adult forms is much more difficult. The ovary and spermary are alike single foliated or lobulated organs, and the sperm mother-cells project from the surface of the spermary as do the ova from the ovary, so that from the gross appearance alone, it is not easy to distinguish the two generative glands. When examined as opaque objects, with a lens or with a compound microscope the same difficulty is experienced, but if treated by any of the approved histological methods the true nature of the elements in each case unmistakably appears (Pl. VII, fig. 27 A, 29 A and 28, 30).

After one has become accustomed to distinguish the sexes by dissection, the differences observable by the eye or with a

simple magnifier, are, in most cases, sufficient to make the diagnosis quite certain. In perfectly fresh specimens the spermary is semi-translucent and has a watery appearance, while the ovary is much more opaque owing to the food yolk in the ova. In hardened specimens this difference is lost, however, so that the determination must be made by comparing the size of the gonads, and the relative size of the ova and the sperm mother-cells. The ovary is always larger at the same stage of development than the spermary, and usually the ova are larger than the sperm mother-cells (Pl, VII, fig. 28, 30). If one has but a single specimen or is not accustomed to determine the sexes, the safest way is to make a histological examination.

In plate I, it is seen that the proportions of the sexes are markedly different, apart from the greater slenderness of the female. It was hoped that by a careful comparison of certain definite and easily determined proportions some guide might be found by which the sexes could be distinguished at all seasons and independently of the transient sexual characters at the spawning season. Careful measurements were made of specimens that had been subjected to the same treatment, in fixing and hardening so that the variations due to different reagents should not complicate the problem. Except for the lake lampreys taken in the breeding season where the sexes could be distinguished easily, each specimen measured was sufficiently dissected to determine with absolute certainty the sex. The results of the measurements in all the different forms studied, adult and larval, are given in the following table :

TABLE showing the total length of the lake, the brook, and the sea lamprey and the larva; also the distance in thousandths of the total length from the tip of the oral disc or dorsal lip to the base of the first dorsal fin, and to the vent; also from the vent to the tip of the tail. For the purpose of comparing the total length in the various forms and the proportions of like parts of the body.

THE LAKE LAMPREY IN THE SPAWNING SEASON.

MALES.				FEMALES.			
Total length in Millimeters.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail	Total Length in MM.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail.
365	520	753	247	330	515	760	240
328	518	737	263	310	516	758	242
310	516	735	265	305	541	738	262
345	507	739	261	345	550	768	232
320	506	750	250	335	537	758	242
300	500	733	267	335	537	746	254
328	518	731	269	315	507	761	239
340	514	741	259	305	557	780	220
310	500	725	275	300	533	750	250
275	501	728	272	310	532	758	242
Av. 322	**510**	**737**	**263**	**319**	**532.5**	**757.7**	**242.3**
THE LAKE LAMPREY OUT OF THE SPAWNING SEASON.							
250	540	760	240	350	514	757	243
395	524	747	253	410	512	749	241
405	518	740	260	420	547	750	250
365	548	780	220	281	509	730	270
375	546	746	254	310	500	726	274
378	579	740	260	240	512	730	270
270	500	722	278	285	526	736	264
305	524	737	263	250	520	740	260
370	492	730	270	350	542	743	257
Av. 346	**530**	**744.6**	**255.4**	**321.8**	**520**	**740**	**260**
JUST TRANSFORMED LAKE LAMPREYS.				LARVAL LAMPREYS.			
140	485	714	286	185	502	730	270
141	500	700	300	132	507	719	281
150	500	700	300	125	504	728	272
152	493	700	300	122	524	739	261
155	500	700	300	108	518	740	260
122	491	713	287	112	499	714	286
135	481	703	297	129	488	720	280
127	500	700	300	135	496	718	282
143	517	720	280	135	496	718	282
145	510	717	283	127	504	708	292
Av. 141	**497.7**	**706.7**	**293.3**	**131**	**503.8**	**723.4**	**276.6**

SEA LAMPREYS FROM LAWRENCE, MASS., IN THE SPAWNING SEASON.

MALES.				FEMALES.			
Total length in Millimeters.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail.	Total Length in MM.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail.
575	525	747	253	645	527	752	248
670	507	731	269	680	519	735	265
670	507	731	269	755	516	728	272
630	523	738	262	680	514	735	265
700	521	728	272	790	508	734	266
690	514	739	261	660	530	742	258
690	524	731	269	667	539	749	251
740	500	736	264	675	518	733	267
630	523	746	254	715	503	741	259
725	538	744	256	755	529	754	246
Av. 672	**518**	**737**	**263**	**702**	**520**	**740**	**260**
BROOK LAMPREYS IN THE SPAWNING SEASON.							
170	470	718	282	150	533	733	267
167	491	718	282	150	502	720	280
152	513	737	263	160	512	725	275
143	503	706	294	150	513	733	267
148	485	709	291	150	520	733	267
156	512	705	295	145	504	724	276
150	500	720	280	150	500	733	267
167	480	731	269	163	521	724	276
150	486	700	300	155	530	722	278
150	500	701	299	162	512	722	278
Av. 155.3	**494**	**714.5**	**285.5**	**157.5**	**514.7**	**727**	**273**

In each case the specimens were measured without selection, consequently the various sizes are represented as in nature. All the specimens measured had been hardened in Müller's fluid and alcohol, except a few of the lake lampreys out of the spawning season. Part of those were hardened in picric-alcohol and alcohol. Only nine of each sex of the non-spawning ones were in the collection, consequently only nine could be measured. In all the other cases ten were measured. The sexes of the just transformed and the larval lampreys were not separated.

An examination of the table for the lake lampreys in the spawning season will show that the relative proportions of the male and the female shown in the frontispiece of this article

hold good for the lake lampreys generally in the spawning season, and expressed in words the table shows that the differences are as follows: (1), That the average length of the male and the female lake lamprey is approximately the same, being a little greater in the male. (2), The distance of the base of the first dorsal fin from the tip of the head is considerably greater in the female than in the male, or in other words the first dorsal fin is nearer the head and farther from the tail in the male than in the female. (3), In like manner the distance from the tip of the head to the vent is considerably greater in the female than in the male, that is, the abdominal cavity is considerably more extended in the female than the male, and, (4), the tail is consequently shorter. This table shows also, as do the others, the very great individual variation, so that any conclusion which might be drawn from the averages in the table might be invalidated in any individual case. It seems to the writer, therefore that for the determination of species of lampreys, the proportions of fixed parts of the body are not of great value.

Upon comparing the averages in the table for the non-spawning lake lampreys there appears the remarkable fact that, apart from the average greater total length of the male, the proportions are exactly reversed from those obtaining in the spawning season and the dorsal fin in the female is somewhat nearer the head than in the male, the abdomen shorter and the tail longer.*

In order to increase the range of comparison, tables are added of the just transformed lake lamprey, larvæ, and the true sea lamprey.

A glance at the averages for the just transformed lamprey will show that its tail is relatively longer than in the adult, the abdomen shorter, and the first dorsal fin nearer the head. The averages given for the larva are more nearly like those of the non-spawning adult than are those for the just transformed ones.

* The results obtained in this table were so unexpected that all of the specimens were re-examined and remeasured to make sure that the females had not been put inadvertently in the column marked males.

The table for the sea lamprey shows clearly not only average greater length but also in each case the greater length of individuals as compared with the lake lamprey. If one compares the sexes it will be seen that the average female is longer than the average male, thus reversing the conditions obtaining with the lake lamprey. The proportions of the body in the male and the female are more nearly alike than in lake lampreys, but the variations are in the same direction as with the male and female of the lake lamprey.

THE BROOK LAMPREY.

Petromyzon branchialis Linnæus, (1758) *Ammocoetes branchialis*. Cuvier, (1827). Plate IV.

Until the spring of 1886 the brook lamprey was not known in North America outside the Mississippi Valley (Jordan '85). The reason for its non-discovery here before, is due to the fact that so far as is known to the writer, it has never been taken on the fish of the lake, and so far has only been found during the spawning season and immediately after transforming in the autumn. Although the spawning grounds of the brook and the lake lamprey are the same, the time of spawning of the brook lamprey is earlier than that of the lake lamprey the two forms never appearing together. This added to the facts that at the earlier time the water is liable to be high and often turbid, and that the size is small, the numbers comparatively few and the coloration inconspicuous, it will be readily seen why it might escape observation almost any where.

In the spring of 1886, while trying to determine the earliest appearance of the lake lampreys on the spawning ground, three male brook lampreys were found by Prof. S. E. Meek and the writer. They were compared with specimens from the Mississippi Valley and found to agree, and in our preliminary paper at the American Association for the Advancement of Science ('86), one of the points made was "The discovery of *Ammocoetes branchialis*, [the brook lamprey] east of the Mississippi Valley."

By comparing the mouths of the lampreys in plate VI, the character of the dentition will be seen to differ greatly from

that of the lake and of the marine lamprey. This difference in dentition, and perhaps also some other considerations, have led some zoologists to divide the genus Petromyzon into two, *Petromyzon* and *Ammocoetes*, and in this case the brook lamprey is placed in the latter genus.*

In size the brook lamprey varies from 140 to 200 millimeters. The color is nearly uniformly dark in the dorsal half and gradually changes almost to white on the ventral surface. The two dorsal fins are said to be continuous with only a sharp notch between them. As the description of this form in America has been based entirely on specimens taken at the spawning season (Jordan, '85, p. 294), the two dorsals could not be described otherwise than as continuous. But, as with the male lake lamprey, this is a feature of the spawning season. In just transformed ones taken in October, there is a considerable interval between the two dorsals, with only an exceedingly low ridge connecting them, a ridge which in the fresh specimen is very difficult to make out. The figure given is of a preserved specimen (Pl. IV, fig. 13).

The brook lamprey of North America is believed by Jordan to be the same species as the brook lamprey of Europe ('85,

* It seems unfortunate to the writer that, if the genus Petromyzon must be divided, some other name could not have been found for the brook lamprey. When larval lampreys were not known to be the tadpole stage, so to speak of the lampreys, but supposed to be entirely different forms, they were put into an independent genus and called *Ammocoetes*. Upon the discovery, by A. Müller ('56), that the animals previously placed in the genus *Ammocoetes*, were merely a larval stage of a lamprey he made the following suggestion, p. 332: "Somit ist nachgewiesen, dass aus den Neunaugen die Querder entstehen, und dass die Querder zu Neunaugen werden. So sind denn auch die Querder, wo sie sich im Systeme bliken lassen, wegen Führung des falschen Namens anzuhalten, und als Unmündige ihren respectiven Eltern zu unterstellen. Der Name *Ammocoetes* kann fortan nur die Larven der Neunaugen bezeichen, wie *Gyrinus* die der Frösche." Milne-Edwards supports this suggestion and urges that the term be used for the larvae of the Petromyzontidae as the term "tad-pole, gyrinus," is used for the frog's young (Milne-Edwards, '57, tome 2, p. 246). This suggestion has been adopted by nearly all morphologists, and the word is frequently used as an adjective, thus ammocoetes stage, ammocoetes form, etc.

p. 294). Of the European brook lamprey, Seeley ('86, p. 427), says that the dorsal fins may or may not be continuous. He does not give the season when they are continuous and when not so, but it may be inferred that they would be continuous in the spawning season and not in others, as with the American brook lamprey. If the European and North American brook lampreys are really the same species, the distribution is remarkably wide, something as with the marine lamprey ; it is also apparently less susceptible to environment than the marine lamprey, for it has apparently been practically unaffected by the special environment of the inland lakes. Certainly also the conditions prevailing in the Mississippi Valley must differ greatly from those found in Europe.

SPAWNING AND THE STRUCTURAL MODIFICATIONS PRECEDING IT.

Structural Modifications.—Besides the change in the gonads (ovary and spermary) there occur marked external and internal changes. Among the most striking of the internal modifications is the gradual change of the liver from the characteristic hepatic color to a bright green. With some examples in which the ova had not yet been shed, there were patches of green intermingled with the ordinary liver color, but in all the green color appears throughout the entire organ before the spawning is completed. This green coloration of the liver appears to be due to the occlusion of the bile ducts and the retention of the katabolic products of the organ. In other than the breeding season, green spherules of liquid of exactly the same color may be found in great abundance in the terminal third of the intestine.

To the unaided eye the change in the liver is simply one of color, but with the alimentary canal the striking change is the diminution in size. From a tube 15 to 20 millimeters in diameter in the lake lamprey, it atrophies to one of 4 or 5 millimeters or even less (Pl. VII, fig. 27, 29, 31–32). The atrophy takes place within two weeks, and begins at the terminal extremity, and extends gradually cephalad until the whole canal

appears like a thread. As no food is taken during the spawning season there is no necessity for digestion, and in the female there is no room for the intestine when the ova are completely matured. This is not the cause of the atrophy, however, for in the male the increase in size of the spermary is less marked than of the ovary in the female, leaving plenty of room for the intestine, still it in many cases is as markedly atrophied as in the other sex.

While the atrophy of the alimentary canal is going on there are certain hypertrophies taking place, differing somewhat in the two sexes, and in the two species. In the male of the lake lamprey there occurs a great increase of the connective tissue along the dorsimeson. This begins about opposite the middle branchiopore and extends to the dorsal fins. This hypertrophy gives rise to a rounded ridge along the back, thus adding a very striking feature to the spawning male (Pl. III, fig. 5, Pl. VII, fig. 31). As an extension of this hypertrophy, the two dorsal fins are approximated to complete fusion in most cases, but apparently no new fin rays are developed. The increase in the connective tissue along the dorsimeson in the female is not marked, except that perhaps the two dorsals appear somewhat approximated. With the female there is a marked hypertrophy in the tissue around the vent thus giving rise to a kind of notch, there is also developed a fin-like fold between the vent and the caudal fin making the caudal fin appear to extend to the vent as in the larvæ of 15 to 20 millimeters in length. In both sexes the urogenital papilla is always present, but in the breeding season it is extended in the male so as to project beyond the level of the body (Pl. III, fig. 6–8).

The abdomen of the female increases markedly in diameter to accommodate the maturing ova ; also as shown by the preceding tables, there seems to be an actual increase in the length of the abdomen, thus shortening the tail. With the male, on the other hand, the abdomen appears to become relatively shorter and the tail longer.

The coloration of the lamprey is very modest out of the breeding season, but in the breeding season there is a great

addition of pigment which appears in the cells of the epidermis, the pigment of the corium remaining about the same. This pigment is yellowish and between the darks spots the color instead of the usual dull gray appears a bright yellow, in some almost golden, thus giving a very striking and handsome appearance. As is common in the lower forms, this coloration is more marked in one sex than in the other, but it is a curious and so far inexplicable fact that some years it is the male that appears in the gorgeous dress while during other years it is the female. For example, during the present year the females of both Cayuga and Seneca lakes were brighter by far than the males, while in 1886 when special note was made of it, it was the males that were more brightly colored.

So far as comparisons are possible the sea lamprey appears to undergo the same changes preparatory to spawning that the lake lamprey does. The specimens personally studied were on their way to the spawning ground and had not reached the same and the changes were not yet completed, but the ridge becomes so prominent during spawning that it has been noticed by fishermen.

With the brook lamprey the changes in the liver are like those occurring in the lake lamprey. The change in the alimentary canal may not be quite so striking as with the lake lamprey. Sufficient material out of the breeding season has not yet been secured to settle that question. In the male the only observed external modifications are the apparent fusion of the dorsal fins, and the considerable elongation of the urogenital papilla. With the female there is the marked anal notch and an apparent anal fin but it is not connected with the caudal fin.

The very striking appearance in the female is due to the swelling in the second dorsal fin thus filling the space between the two. At the first of the season this is merely an œdema, which appears light or semi-translucent, but later, in many cases, it becomes infiltrated with blood and is bright scarlet (Pl. IV, fig. 11–14).

No dorsal ridge is developed in either sex, and apparently the general coloration of the body is unchanged.

Nest Building and Spawning.—As spring approaches the ovary in the mature lampreys increases greatly in size by the addition of food yolk to the multitudinous ova. With the male the actual increase in size of the spermary is not so great, but the ripening sexual products act as a stimulus in both sexes, urging them to complete the cycle of existence by seeking again the clear brooks, far from the lakes, where they themselves began an independent existence several years before. Apparently they start out independently from the various parts of the lake, each one forsaking its prey, and swimming vigorously or stealing a ride by attaching itself to the bottom of some boat moving in the right direction. On they go until the current of the inlet gives them the clue, and they follow it. Frequently also ordinary fishes, bound on the same errand, throng the streams, and then the lampreys, with their inherent desire to be taken care of by the labor of others, fasten to the larger fishes and are carried along up the stream. It not infrequently occurs that from the natural inclination of the stream or from some of man's obstructions, there are rapids or dams to be surmounted. Nothing daunted the lamprey swims up just as far as possible by a tremenduous effort, grasping a stone or other solid so that he should not be carried down stream again, rests for a while and then by a powerful bending and straightening of the serpentine body, a leap is made in the right direction and what is gained is saved by again fastening the mouth to a solid object. This goes on until the obstacle is surmounted if it is not too great. Then without waiting to think of the victory gained the lamprey pushes on up the stream sometimes 8–10 kilometers until clear water and numerous ripples are found. Just above some ripple, the lamprey begins to make ready a secure place for the beginning of a new generation.

From the numerous observations on the brook lampreys it appears that they are somewhat communistic or gregarious, and join in considerable numbers, sometimes 8 to 10, to make a common nest, but with the lake lamprey, while four or five are sometimes in a large nest it more frequently happens that but a single pair is present. If the situation is especially fav-

orable one may see five to ten nests within a small radius ; and perhaps the explanation of the very large nests may be that several pairs commenced to build in such close proximity that before they had finished, the nests run together thus producing a single large nest with two or more pairs. Whenever the nest is especially large it has an appearance of a rounded ditch, across the stream not parallel with it.

If one observes the nest building throughout the season it will be seen that those found earliest and those farthest up the stream, contain but one lamprey, and usually the single one is a male. It would thus appear that away down in the very stem form of the vertebrate series the male is the house-builder and takes the lead in preparing for the offspring. The female is not by any means a sluggard, however, and when she joins the male, sets to work with all her might to help complete the nest.

As stated above, the place most commonly selected for a nest is in moderately swift water just above ripples. Now to build the nest the animal has neither hands nor feet, only a mouth, but the mouth is perfectly adapted for grasping by suction and so the lamprey heads up stream, fastens to a stone, the stone being frequently more than twice as heavy as the animal itself. Then with powerful backward or sidewise swimming movements the stone is loosened and dragged down the stream a distance a little greater than the length of the animal, here it is deposited and another grasped and carried down, and so on. If the stone is small it may be carried down by being lifted free from the bottom (Pl. VII, fig. 39). Sometimes a stone will not yield to the most vigorous tugs. In such a case it would be very pleasant to say that two or more joined forces. Two may attach to the same stone if it is large but two have never been seen by the writer to actually join in moving a stone. On the other hand the smaller stones are removed from around the larger one, and from time to time the efforts to remove the large one are renewed until finally it yields to the combined force of the lamprey and the current.

The nests are usually somewhat oval and the diameter parallel with the stream somewhat greater than the length of

the lampreys making them. The central part is usually 15 to 20 centimeters deeper than at the edges so that the whole is nest-like or dish-like in appearance. At the lower edge is always a pile of stones which were carried down in making the nest. As the stones from the upper edge and sides of the nest are loosened the sand is carried down by the stream and lodges in the deepest part of the nest. After the nest has a considerable pile of stones at the lower edge and a good layer of sand in the bottom it is ready to receive the eggs. In ovulation the female secures herself firmly to a large stone at the side or upper edge of the nest so that the body can extend out into the nest, then the male fastens to the female, somewhere near the head, he then winds himself half way around the female, whereupon the two bend their tails downward and stir up the sand by the most vigorous movements. Simultaneously the ova and the milt are forced out in a stream and mingle in the water, and also mingle with the sand. The eggs are coated with an adhesive substance which enables them to adhere to any solid they come in contact with, consequently they stick to the particles of sand that have been stirred up in the water and, as the eggs are themselves heavier than water and made still more so by the particles of sand to which they adhere, they quickly sink to the bottom before the current can carry them below the nest ; they are also partly covered by the depositing sand. If many eggs have been extruded, all are not covered and the bottom of the nest may be quite thickly strewn with them. In nearly all cases some remain uncovered. After the pair have "shaken together" as the ovulation is called, they separate and commence at once to remove stones from the upper edge and sides of the nest and pull them down stream as if to enlarge the pile at the lower edge. This was at first puzzling, for the nest is apparently completed before the ovulation begins. The explanation soon became evident, for while immediately after "shaking together" there might be many uncovered eggs, in a very short time they all disappeared, being covered by the sand that was loosened by the removal of the stones and carried down the stream by the current.

The ovulation is repeated at intervals until the eggs are all extruded. If during the spawning the lampreys are disturbed so that one or both leave the nest they soon return. After the spawning is completed, however, they leave it for good and a newly arrived pair may utilize it and thus save themselves much labor. This is proved by catching a pair in a nest and finding the nest occupied by another pair on returning some days later. It is also proved by the fact that from the same nest, during the middle and latter parts of the spawning season, one can obtain eggs apparently but just laid and in the earliest stages of development, and embryos 8 to 10 millimeters in length.

The duration of the spawning season for the brook lamprey is about two weeks. They appear earlier than the lake lampreys and all disappear before the lake lampreys arrive. Frequently the lake lampreys utilize the nests of the brook lampreys as they do the nests of earlier pairs of their own species, as described above The time for the spawning of the brook lamprey usually begins about the 8th of May and lasts till about the 20th. The lake lamprey usually appears about the 25th of May and disappears about the first of July, the height of the spawning time being about the 10th of June. The time varies from year to year and corresponds in general to the advance of the seasons.

As one watches these humble creatures with their pigmy brains and observes with what exactitude they recognize that "to rule nature one must obey her," there comes to one the feeling that the germ, at least, of the highest achievement is present in these our lowly vertebrate allies and that the abyss separating us from them is not so wide after all. If it is urged that all this precision and the resulting efficiency is due to blind instinct then it may be answered that an instinct which guides its possessor to apply the appropriate means to accomplish a desired end, to overcome difficulties not previously encountered by the race and guides it to make the most of favoring circumstances whether they be common ones or those never before utilized, then it must be said that such a guide is a pretty good thing to have after all, and about as valuable

to its possessor as something else, although the something else may have been dignified by the name of reason.

Fate of the Adult Lampreys after Spawning.—As to what becomes of the lampreys after spawning the opinion of authors is conflicting. A. Müller ('56) says concerning it that from the dead ones found at the close of the spawning season and from the fact that in the ovary were eggs of only one size, probably death followed the egg-laying as in case of many insects. Couch ('65), in his work on the fishes of the British Isles remarks concerning this point (Vol. IV, p. 391–392), "As this species of lamprey [the sea lamprey] enters rivers for the purpose of spawning in the spring, this is the season of highest perfection ; but immediately after the shedding of the roe so great a change takes place, that they are not only weakened and emaciated, but it has been believed that death is commonly the result. But this last supposition at least is not correct. . . . . Soon after spawning the parent fish returns to the sea." Seeley ('86), says concerning the sea lamprey, "After spawning the fish is exhausted and goes down to the sea." Of the river lamprey he says, "After spawning the lampern usually dies ; " and of the brook lamprey, "After spawning the old fishes probably die." Benecke, ('80–81), as quoted by Goode ('84), remarks upon this point, "After the eggs have been deposited, the lampreys die." The proof in each case is not proof, but probability, from each author's standpoint, the strongest argument being that of A. Müller,—that the ova in the ovaries are all of the same size.

Unfortunately the fate of the lampreys after spawning has not been determined by the writer, although special pains were taken to determine it. Several facts seemed to indicate that, with both species, most of them return to the lake after spawning, for in the middle and later part of the season many lampreys are found going down the stream or attached to stones below the nesting places. On examination such lampreys were always with empty gonads. As to their death on the spawning grounds, especial care was taken to look for the dead, but in all the years of investigation not more than 10 dead ones were seen. This does not indicate the number that

might have actually died, however, for birds of prey hovering over the water would be very liable to catch any that were *in extremis*. Nature has so many ways to dispose of dead bodies that the number seen even on careful investigation is small, even though the actual mortality may be great.

In the last part of the season many were affected by saprolegnia, especially where the epithelium had been injured by the attachment of another lamprey. An additional argument in favor of the death of the lampreys after spawning, is the condition of the alimentary canal and the liver. There would need to be almost a new building of the alimentary canal. And then enforcing the argument from the absence of small ova in the ovary after spawning it is to be said that even in the larva the eggs are of considerable size (Pl. VII, fig. 38), so that if the lampreys that had spawned were to return to the lake and re-acquire ova a greater development in the ovary would be required than takes place between late larval life and sexual maturity ; a development requiring from two and one-half to three and one-half years in the lake lamprey.

An effort was made to determine the matter experimentally by transferring lampreys that had spawned to water containing cat-fish (*Amiurus nebulosus*), as the lampreys seem particularly fond of cat-fish. The conditions were very unnatural as the only available place was a cold spring. The cat-fish soon died and the lampreys also, without attempting to feed on the live or dead fish. It seems to the writer that the experimental method is the only one promising satisfactorily to settle this vexed question, a question important alike from the scientific and from the economic stand-points. If a pond through which the water from the stream in which they spawn or one connected with the lake were stocked with cat fish or suckers (*Amiurus* or *Catostomus*), fishes which are frequently attacked by lampreys, and then if lampreys were placed there after spawning one could determine the duration of life after spawning under natural conditions of water and plentiful food. There is no difficulty whatsoever in keeping lampreys alive and in good condition out of the spawning season even in a large aquarium where there are other fishes. Indeed the lam-

preys are so vigorous and aggressive that, when hungry, they will attack the ganoid fish, *Amia calva*, and rasp away the scales sufficiently to extract blood from the amia. If they naturally return to the lake and resume their ordinary mode of life there should not be the slightest difficulty in determining it under the natural conditions just mentioned. It is hoped that suitable facilities may be afforded at some future time to settle definitely this important question and also several others that have arisen in the study of the various stages in the life history of these animals.

DEVELOPMENT OF THE OVUM AND LARVAL LIFE.

The ripe ova are about one millimeter in diameter and nearly spherical. They are very opaque from the abundance of opaque food yolk, and each is surrounded by a thin layer of material which is very adhesive upon exposure to either air or water, consequently the eggs adhere to whatever solid body they come in contact. The adhesion is not very permanent, however, as after a day or two they are easily detached.

Some eggs of the brook lamprey were fertilized and kept until the larvæ were hatched. The segmentation is total and unequal as in the amphibia, and the development proceeds with great rapidity ; after eleven days the heart beats are plainly visible. In 14 days the mouth is shark-like and on the ventral side, and the blood vessels extend around the gill slits. In 18 days the eyes are clearly shown, respiration and the movements of the velum are evident and the mouth has assumed the larval appearance with the hooded dorsal lip so characteristic of the older larvæ. The fins are represented by a continuous fold from a point about opposite the 4th branchiopore along the dorsimeson and around the tail on the ventrimeson to the vent. In swimming the larva goes with a wriggling motion ; it holds itself dorsal side up as do the older larvæ when swimming and like the older ones rests on the side when quiet.

As was shown by Calberla ('77), the nervous system develops as a solid cord and becomes a hollow tube only later in the course of development. In this respect the lamprey

agrees with the teleosts and the ganoids, so far as they have been investigated (Calberla, '77, Balfour, '81). Other references to the embryology of the lamprey will be found in the bibliography at the end.

In nature the young larvæ live in the sand in the bottom of the nest where the eggs were deposited by the parents. Sometimes the larger ones are found most abundantly in the sand and gravel under the pile of stones bordering the lower edge of the nest. This may have given rise to the prevalent notion that the pile of stones is the real nest. One can obtain the embryos very easily by shoveling up the sand from the bottom of a nest. If water is then added to wash away the mud, and the sand is shaken lightly, the eggs or embryos or both appear on the surface, and are readily detected by the light color of the eggs or the greenish color of the food yolk in the embryo of 8 to 10 millimeters. After the larvæ are 10 to 15 millimeters in length it is far more difficult to secure them as they are less conspicuous and far more active. Then too, they exhibit already the habits of older larvæ and very quickly disappear in the sand.

The exact time the larvæ remain in the nest and the stage of development reached by them before leaving it is not known with exactitude. Already on July 31st, larvæ 30 mm. long were found while searching for large larvæ. A few days later a thorough exploration was made by my assistant, G. S. Hopkins, D.Sc. both in the nests and in the sand banks at the concavity of the stream where the larger larvæ are found throughout the year (Pl. VII, fig. 40). None could be found in the nests at the bottom of the stream, but in the sand at the side of the stream many of all sizes were obtained, some of them being only 16 millimeters in length. Consequently it is believed that the larvæ remain in the nests only about one month or until they attain a length of 12 to 15 millimeters. Whether they voluntarily leave the nest or whether the rapid current of some sudden rise in the stream, as after a heavy storm, washes them out of the nest is not known. It is believed, however, that they leave the nest voluntarily, for, on account of the conformation of the nest, any moderate in-

crease in the stream would tend to cover the larvæ still deeper.

Larval Life.—After the larvæ leave the nest they wander down the stream until some suitable place composed of sand and mud is found. This suitable place is most often in the concavity of the stream where the water flows slowly and there is not great danger of being washed away by every freshet. Judging from specimens in the laboratory that were placed in glass vessels with water, and sand from the native habitat, each larva has a canal or burrow of its own. This burrow usually opens on the surface of the sand. In this burrow the larva remains, changing its position at will and also making a new burrow with a new surface opening as inclination or necessity demands. In those observed in a glass vessel where there could be no doubt, the canal was curved, the convexity of the curve being downward (Pl. VIII, fig. 49). The larva was curved correspondingly ; but the dorsal side was always up as shown in the drawing. Often in moving to and fro in the canal the tail would be higher than the head. If disturbed the larva leaves the burrow and worms itself through the sand with great alacrity. They do not leave the protection of the sand if they can possibly avoid it. In their natural home beside the streams, they are usually only a few centimeters under the surface of the sand and frequently not more than 15 to 40 centimeters below the water level. In taking them the sand is shoveled up from the stream and carried out to the shore and placed on the bank or upon something else so that the water may drain away. As soon as the sand is pretty well drained, any larvæ present wriggle out to the surface where they can be seen. To obtain the smaller ones it is necessary to take somewhat more care and spread the sand out in a thin layer ; sometimes also it is advantageous to pour water over it.

The way in which the larvæ enter the sand from the water and the way they move around in the sand was very easily and satisfactorily demonstrated by placing some of the sand from the native habitat in a glass dish and partly filling it with water. The sand was washed to avoid turbidity then a

larva introduced. If the creature is vigorous it almost immediately commences to bury itself, and in the following manner: It stands almost vertically on its head and then makes most vigorous swimming movements. At the same time the head with its hood-like dorsal lip is twisted from side to side something as one turns the hand in trying to force an awl into wood or leather. In a short time the animal will bury itself to about the extent of its branchial apparatus, that is until the sand affords a kind of hold for it. The animal then ceases to go directly downward, but with a serpentine movement, constantly twisting the head from side to side to open the sand, it goes more nearly horizontally till the body is entirely covered. Once in the sand the creature moves around with great ease, the head and hood-like dorsal lip serving by their stiffness and mobility to part the sand. It soon makes a burrow and the opening to the surface of the sand. In this burrow it can move to and fro at will. The sand seems to be packed in some way so that it does not cave in and fill the canal.

In discussing the habits of the larvæ it is frequently stated that they have a great dislike to light and swim around in the vessel in which they are placed until exhausted and they die. From my own experiments the larvæ do not seem to have a great dislike to light, but rather there is a sense of insecurity when not covered by the sand. Experiments were carried on for weeks with those in glass vessels to see if, when the burrows were next the glass, and that side turned to the light the larvæ would move away from the light, as they could very easily do if desired. Sometimes they would make a new burrow on the side from the light, but nearly as often the change would be made from the shaded to the light side. It thus appeared that if the animals were protected by being in a normal habitat in the sand the restlessness mentioned by authors as due to light would not be observed. Furthermore one was kept alive in a small globe, hanging, glass aquarium with other aquatic animals from Christmas till the following May. In it there was no sand present and the animal was thus constantly exposed to the light throughout the day.

Whenever a larva swims it is always dorsal side up, but in resting on the top of the sand or on the bottom of a vessel of water it lies on the side. Apparently the side on which it rests is a matter of chance as it is sometimes the left and sometimes the right.

Comparison of the Larva with the Adult.—As one watches the development of a lamprey's ovum it is seen that in a very short time, 10 to 15 days, the embryo assumes characters markedly like its parent ; but a closer study will show very marked differences. Instead of a circular, sucking mouth armed with teeth, the mouth is hooded and the entrance guarded by a very perfect sieve (Pl. VI, fig. 22), and between the mouth and gills will be seen a reddish body that moves to and fro rhythmically and in unison with the movements of the branchial apparatus.

If the branchial chamber is explored the seven branchial openings on each side will not be found to open, each into a separate sac or pouch, but into a large common chamber, a chamber serving also for an œsophagus. The eyes, too although visible do not reach the surface, but remain quite deeply imbedded. Many other structural differences occur, but a sufficient number have been named. In habits the difference is as striking as the difference of structure ; the parent is a free-booter, the offspring lives an orderly and isolated life. It is no wonder that naturalists and fishermen should have agreed that they were different animals ; that they were different stages of the same animal probably did not enter their minds.

So strikingly unlike are frogs and their young, the tadpoles, that it would be deemed almost incredible that one is the offspring and would assume the appearance of its parent if the facts were not forced upon every one that is at all observant. The transformations in insect life, too, are even more marvelous, but from their frequency are taken as matters of course. Apparently, a fisherman and naturalist of Strassburg Leonhart Boldner in 1666, knew of the metamorphosis of the lampreys, and that the larvæ were larvæ and not distinct animals. But this was lost sight of, and the knowledge

of the scientific world dates from the discoveries and the publication of A. Müller, 1856. (See note on p. 437 above).

Duration of the Larval Period.—The time required for the larva to prepare itself for adult life is not known. It has been estimated at three to four years. The reasons for assigning that time are: The larvæ that may be obtained from the natural habitat at any season of the year are of such varying sizes that it is believed that from three to four generations are represented. The first of September for example, one may obtain from the same bank or bed, as the fishermen call it, lampreys in various stages of transformation, larvæ about two-thirds as large as the transforming ones and so on down to the generation of that year, which are from 15 to 40 millimeters in length. This like the supposed death of the adults after spawning is one of the questions that must be determined experimentally. As the larvæ are easily kept for six months to a year in an aquarium with sand, it would doubtless be very easy to keep them from the egg until transformation, by imitating closely the conditions obtaining in their native home.

Transformation and Duration of Adult Life.—When the larvæ attain a length of 120 to 160 millimeters for the lake lamprey or sometimes as great a length as 200 millimeters for the brook lamprey, they transform to the adult condition. The brook lamprey does not apparently increase in length after transformation, for many of the transformed ones at the spawning season are of less size than the just transformed ones. There is, however, some increase in the bulk of the body, and a considerable increase in the gonads. As shown in plate vii, figures 35 and 36, the ova and the sperm mother-cells are in about the same stage of development as the lake lamprey six months before spawning. It is believed from this that the brook lamprey attains nearly its full growth before transforming, and that the free life in the water is only about six months, that is from the transformation in the autumn, August and September and perhaps October, till the following May.

The lake lamprey upon transforming is only about $\frac{1}{2}$ to

$\frac{1}{4}$th the length and probably not one $\frac{1}{10}$th bulk of the spawning ones. The gonads are small and the ovary and ova are minute but perfectly recognizable on transforming. The comparative size is given on plate vii. The gonad of the male is very small indeed, and the sperm mother-cells not far advanced. To attain the size and maturity of the spawning ones it is believed that two or three years are required. This conclusion is reached by the size and development of individuals caught in various months of the year. For example, while the lake lamprey is spawning, specimens have been taken from the lake with the intestine large and full of blood and with ova of about half or one-third the size of the mature ones. In others of about 200 or 225 millimeters length the ova are still smaller. The smallest ones are supposed to have transformed six to eight months previously and those next in size a year and a half earlier. The absolute bulk of fishes depends so largely upon the food supply that size of body alone is not a good test of maturity. The size and stage of development of the sexual organs is a safer guide. Following this guide it seems very probable that it requires either one year and a half, two years and a half, or three years and a half for the small, just transformed larva of 150 millimeters to attain a length of 450 millimeters, or rather that ova of the size shown in plate vii, figure 34 A, require that time to reach the size and maturity of the egg shown in 32 A. This question like those previously mentioned can be definitely settled only by rather expensive experimentation. That it has an important scientific interest all biologists will agree ; that it also has a very important economic bearing may be seen also when one reflects how many food fishes are either destroyed or greatly weakened by the parasitic adult lampreys.

The transformation of the larva into the adult is usually described as taking place in a few days. In three or four (en trois ou quatre jours) according to Bujor ('91), for the European brook lamprey (P. planeri, or P. branchialis). The time given by Müller is longer, 10 to 26 days. My own observations accord more with those of Müller. The first external signs of transformation is the appearance of the eyes upon the

surface and the development of the sensory papillae in the characteristic curved line interrupted by the eye (Pl. VIII, fig. 50). Looked at in a strong light the eyes appear in a dorsal view like clear spaces ; looked at from the side the black pigment, especially in the dorsal half, is very evident. The mouth in this stage is precisely the same as the larva to all appearance and so is the general coloration of the body. In a somewhat later stage the eyes are still more evident, but appear dull and as if covered by only a semitranslucent membrane. The mouth has no longer the wide open appearance of the larva but has become greatly contracted ; the dorsal and ventral lips are becoming fused and the oral tentacles arrange themselves as shown in figure 23. The appearance is exactly as if the papillæ or tentacles were to form the basis or foundation for the future teeth. Several days (20) later the eyes are less turbid and the oral tentacles have lost their branched ends and have become blunt papillæ. In one kept in a large glass vessel with sand and stones, changing the water frequently, the changes just described were gone through in 25 days. But it is believed that nearly as many more days are needed to develop the large, clear eyes of the adult form and the enlarged sucking disc with horny teeth ; so that with those investigated by me the metamorphosis cannot be said to go on very rapidly, but rather, very slowly. One of the striking external changes also is the gradual darkening from a brownish gray to a blue black, which is so rich and soft that it appears like velvet. The pineal eye then appears like a snow white, rounded spot. Later it is partly overshadowed by the thickening epithelium and looks dull (Pl. VIII, fig. 50). A striking change in attitude also occurs. The animal rests dorsal side up and not on the left or the right side as with the larva.

Corresponding with the external changes, there are profound internal changes. The intestine no longer opens into the bronchus, but a new œsophagus is developed along the dorsal wall of the bronchus and finally opens cephalad of it very near the mouth. The gills cease to be in a common chamber and are divided, each one forming a pouch which opens to the exterior by the branchiopore as in the larva and into the

common bronchus by a small opening about the size of the external opening. The velum gradually atrophies and soon almost disappears. It is stated by Bujor that in the metamorphosis, the tissues return to an embryonic condition and then are reformed into the tissues of the adult. "Les différents tissus des organes larvaires se régénèrent complètement pendant la métamorphose," (Bujor, '91, pp. 77, 88). Especial care was taken in investigating the transformation to determine something of the activity of the animals and their mode of life. The first transforming ones were obtained the last of August. The last just transformed ones from the native habitat were obtained the middle of October. Aquaria were prepared with sand and gravel, thus imitating as closely as possible the natural conditions. Into these aquaria the transforming animals were placed as they were received and each aquarium carefully labeled with the date and the stage of development. All of the animals that were in good condition very soon disappeared in the sand. Those with a fully developed sucking mouth surrounded by the oral fringe of papillæ (Pl. VII, fig. 19–21), also buried themselves. Some of these were so far advanced that the horny tips to the teeth were already visible with a lens. It is therefore believed that the animals, in nature, remain under the protection of their early home until they are fully armed and ready to get their food in the usual adult fashion.

The activity of the animals seemed not at all lessened. In a vessel of water they swam with the same vigor as untransforming larvæ and frequently like them made vertical leaps of 10 to 20 centimeters to escape from the dish. The respiration seemed in no way interfered with. So far as certain structures are concerned, at least, there seemed no tendency to return to an embryonic condition. The ova, for example, in 100 millimeter larvæ have the unmistakable characters of the ova in young adults. None of these characters are lost during transformation. Certain profound changes take place, that is certain, but these changes appear to the writer rather the additions to or rearrangement of tissues common alike to the larva and the adult, new structures also appear and purely

larval organs like the velum atrophy. So far as the liver and its duct are concerned it is almost universally stated that in the European brook lamprey the bile duct loses its connection with the intestine upon transformation. This is not the condition in the lake lamprey and in many examples, at least of the sea lamprey. It is only upon the atrophy of the intestine at the breeding season that the bile duct is occluded. Then the liver assumes an emerald green color as stated above (p. 438). From the numerous observations made by the writer on transforming lake lampreys and sea lampreys from the Susquehanna River, there is not a period of quiescence comparable to the pupa stage of insects ; such a period would be expected with so great a histolysis and subsequent histogenesis as described by Bujor ('91) for the European form of the brook lamprey.

In collecting the transforming lampreys the same method is employed as described above for the untransforming larvæ. It is well, however, to have a dip net with a long handle, for the transforming ones more readily leave the sand when it is disturbed by the shovel, and attempt to swim away in the stream. With the dip net these may frequently be caught.

Up to the present time there has been no way discovered of distinguishing the larvæ of the lake and of the brook lamprey. As the two species occupy the same spawning ground and sometimes spawn in the same nest great care is necessary in order not to confuse the two. After the larvæ leave the nest they apparently go to the same sand bed. There are certain peculiarities about the one figured in plate iv that might lead one to diagnose it as the larva of a brook lamprey. Here again, only a carefully conducted experiment would give definite and reliable information.

If one can keep the transforming ones alive until the dental papillæ appear on the oral disc the distinction is as clearly marked in the two species as in the adult, for there is the same definiteness of arrangement, and the same arrangement of dental papillæ in the young as in the horny teeth of the adult. The general appearance of the brook and the lake lamprey is also as strikingly unlike at this stage as in any subsequent one.

ECONOMICS.

From the human stand-point, beneficial or injurious, as applied to an animal or plant relates solely to the supposed advantage or disadvantage to the human race that it subserves. No doubt from the economical stand-point of the animal or plant, judge and prisoner would change places. In this economical consideration two questions arise: First, in what way does this animal or plant subserve man in supplying food or clothing and secondly, does it destroy, for its own use, food or clothing that might otherwise be utilized by man.

To answer these two simple questions it is only necessary to find out the food of an animal, and also the animals for which it in turn serves as food.

Food and Uses of the Larva.—The food of the larva consists of microscopic organisms separated in some way from the constant stream of water drawn into the combined œsophageal and branchial chamber. It thus appears that in its larval life the lamprey is not injurious to man by destroying food that he wishes, directly or indirectly, to utilize for his own benefit. On the other hand, from the tenacity with which the larvæ retain life they have been found excellent bait for all kinds of ordinary carnivorous fishes. The fishermen along the Cayuga and Seneca Lake inlets make considerable use of the larvæ for bait; this form of bait has not up to the present been much used in the lake fisheries, as apparently its excellence is unknown. At Owego, on the Susquehanna River, however, quite a business is carried on in supplying larval lampreys to fishermen of all kinds, and many are shipped to distant points.

As no distinction is yet known between the larvæ of the brook and of the lake or sea lamprey, all larvæ may be classed as non-injurious and as positively beneficial by serving for bait, and thus in aiding man to obtain food fishes.

Economics of the Adults.—Unlike the larva the adult lamprey is largely or wholly parasitic, and in obtaining its food destroys or injures the fishes used by man as food. It is stated by Günther ('53, p. 133), that the food of the lamprey (*P. marinus* and *P. fluviatilis*) consists of worms and insects,

and fishes to which it attaches itself. He is followed by nearly all authors, more especially in describing the food of the brook and river lampreys. From personal observations, the food of the brook lamprey of the lake region has not been determined, as none have been taken out of the breeding season except those which were transforming. From their small size (150–200 millimeters) and the probable shortness of adult life, the injury to the larger food fishes in any case must be considered slight. This is especially true of the region under consideration, for in addition to the smallness in size and probable shortness of life, they are few in number. While it is not at all difficult to get 200 to 400 lake lampreys from the Cayuga Lake inlet during one spawning season, one must work quite persistently to obtain 75 to 100 brook lampreys.

With reference to the usefulness of the brook lamprey in New York, it may be put down as nil. In England, according to Couch ('65) and Seeley ('86), the adult river lamprey which is very closely allied to the brook lamprey, or specifically identical with it (Schneider, '79, Shipley '87), was formerly much used in the cod and turbot and other deep sea fisheries. It is stated by Seeley that the lamprey fishery begins in August and continues till March, and that in that time as many as 450,000 have been taken and used as bait in one year.

With reference to the lake lamprey, the conditions are quite different from those described for the brook lamprey. In the first place the lake lamprey exists in large numbers, and lives a parasitic life from one and a half to three and a half years. Of all the specimens obtained out of the breeding season, either the digesting part of the alimentary canal was empty or it contained blood. No partly digested worms or insects or small fish or fish flesh were ever found, although diligent search was made; consequently it is believed that the lake lamprey is wholly parasitic during its adult life and lives on the blood sucked from other fishes. From the structure of the mouth and the opening to the œsophagus in the adult, one might also infer that liquid food was used and that this was obtained by suction as with a leech.

From observations on the lampreys in flat sided, glass jars, and by experiments in allowing them to fasten to the hand, the process of attachment appears to be as follows: The oral disc is quite widely expanded and pressed suddenly against whatever the lamprey wishes to fasten to. Almost instantly the mouth is somewhat arched and any water that may be present drawn into the bronchus. The circum-oral fringe of papillæ with the continuous fold of mucosa bordering the fringe, serves to fill any irregularities and make the contact, air and water tight, so that upon lessening the pressure within the mouth the adhesion becomes very perfect. So perfect is it, that such a hard scaled and vigorous fish as the ganoid, *Amia calva*, can rarely prevent the attachment and adhesion although the most violent efforts are made. If they are attached to stones of moderate size, the stone is frequently brought out with the lamprey if the animal is jerked up suddenly. In letting go its hold all that is necessary for the lamprey is to fill the disc with water from the respiratory bronchus, whereupon suction ceases and the animal is free. In feeding, the sharp teeth pressed against the skin of the animal to which it is attached, naturally calls the blood to the place. This hyperæmia is caused even more by the suction. At the same time the piston-like tongue with its powerful muscles and the saw-like teeth soon rasps a hole through the skin. The blood is then sucked from the fish and swallowed. The whole operation is something like the extraction of blood by a leech. The lamprey may remain upon a fish so long as it supplies sufficient nutriment. Sometimes the fish becomes exceedingly pale and weak so that it floats near the surface. In such a case, the fishermen know immediately that there is a lamprey attached to the fish, and, with a dip net, usually have no great trouble in catching both. The birds of prey also make this their opportunity and frequently carry off the floating fish, the lamprey sometimes remaining attached until it has been carried a considerable distance into the air.

According to one intelligent fisherman, who has spent nearly fifty years by the lake, some of the fishes, when a lamprey attacks them, will rise to the surface and turn over on the

side so that the lamprey's head and branchial apparatus are out of water. By this means the lamprey is partly suffocated and lets go its hold, thus freeing the fish.

That the injury to the food fishes is very great may be inferred from the fact that sometimes out of 15 cat fish caught on a set line in one night, 10–12 have great raw sores where a lamprey has attacked them. In the spring, too, when the suckers (*Catostomus*) run up to spawn, very many of them carry a lamprey, and naturally by the great drain of blood that it causes, the fish must be weakened, so that obstacles on the way to the spawning ground are less liable to be surmounted than as if the fish were in full vigor.

As stated above, during a single season over a thousand lampreys were caught in the Cayuga Lake inlet. If these had spent from two to three years infesting the fishes of the lake they probably did more to reduce the number of available food fishes than the fishermen.

In 1891, on account of the lack of rain and the clearness of the water in the streams at the spawning time, conditions were very favorable for determining the number of nests in the Cayuga Lake inlet. This was done for about 10 kilometers, and 400 nests found. If each nest had been inhabited by a single pair, then 800 lampreys visited the inlet for spawing during that spring; but in 1886 over 1000 were known to have been caught from the inlet, and furthermore by direct observation some of the nests are utilized by at least two pairs of lampreys, so that probably the 400 nests represented a visit of 1000 to 1200 lampreys and perhaps more. The males are usually somewhat in excess so that probably there were from four to six hundred females. The number of eggs in the ovary of a lamprey of moderate size was estimated in the usual way by weighing a small piece and counting the eggs in it and then weighing the whole ovary. The eggs present in the whole ovary is then estimated by a simple proportion. In the case mentioned, the ovary was found to contain 65,000 ova. (A sea lamprey from the Merrimac River was found, by the same method, to contain 236,000 ova). If each of the females that were on the spawning

grounds that year deposited 65,000 ova there would have been laid $65000 \times 400 = 26,000,000$. Many of the ova fail of fertilization and many also fail to develop even if fertilized so that of the possible twenty-six million young lampreys from the spawn of a season, possibly not over 4 or 5 thousand reach the sand beds ; and from the further decimation of these the numbers in the lake remain approximately uniform as with other animals in nature.

Ridding the Lakes of Lampreys.—From the foregoing account of the life history of the lamprey it will be seen that it has a single very weak point, viz., leaving the lake and running up the tributaries to spawn. This seems to be the only weak point at which the lamprey can be attacked with a hope of exterminating it. This point is rendered still weaker from the fact that in Cayuga Lake, and in Seneca Lake, so far as explored, the lampreys run up the inlet at the head of the lake only, and do not spawn in the tributaries entering the lake at intervals on each side. Some of the lateral tributaries seem well adapted for the lamprey's spawning grounds ; these streams are used by other fishes, but the most careful exploration under favorable circumstances gave no sign of the lampreys. Also, as will be seen by examining the map (Pl. II), the large creek (Fall Creek) entering the head of Cayuga Lake by a separate entrance, has never been known to contain lampreys. Careful personal search was made for several seasons and inquiry made of those familiar with the creek, but none were ever found or heard of. This may be due to the nearness of the falls in the course of the stream. The creeks joining the inlet (Cascadilla and Six Mile creeks) contain them. Formerly they were very abundant in both, but the water is not now so plentiful and then both extend for a considerable distance through the city. At present it is the main stream that is most frequented and employed by the lampreys for spawning. The lampreys must be destroyed before spawning if they are to be exterminated. Nothing would be easier than to do this. A dam with a fish-way, the fish-way leading into an isolated enclosure where the lampreys could be easily removed and disposed of, or a weir

of some kind could be constructed at slight expense. If this could be continued for three to four years in all the lakes and in the Oswego River, the race could be extinguished and the lake wholly freed from their devastations. So vulnerable is this point in the lampreys defenses, that even in great rivers, where dams exist, the fish-ways could be utilized to free the river of lampreys as well as to allow the more valuable food fishes to run up and spawn. To be sure, in the Merrimac and Connecticut rivers the lampreys have been largely utilized for food, but if one considers the damage these monstrous parasites must do to the ocean fishes it will be seen that too dear a price is paid for the food they furnish. It seems to the writer that from every economical standpoint it would be advantageous to rid the world entirely of the lampreys. It would certainly be greatly to the advantage of the fisheries of the State of New York if all were destroyed. Naturally, however, the student of biology must mourn the loss of a form so interesting and so instructive.

RESPIRATION AND THE RESPIRATORY MECHANISM IN THE LARVA AND IN THE ADULT.

In the lampreys, the respiration is wholly aquatic. They do not come to the surface and take in air as do many fishes. As the dissolved oxygen is only 6 cubic centimeters in 1,000 c. c. of water, while in the air there are 209 c.c. of oxygen in 1,000 c.c. of air, it follows that an animal like the lamprey with a purely aquatic respiration must either be very sluggish, or a very perfect respiratory *mechanism* must be present in order that it may obtain the needed oxygen from the meager supply in the water. In the lamprey there is a very perfect respiratory mechanism. If one considers also the ease and completeness with which the carbon dioxid is eliminated in aquatic respiration, and the fact that with the lamprey, from its habits, only occasionally are great exertion and rapid movement necessary, as in searching for prey and in spawning, with the attendant nest building, it will be seen that the lamprey is very well off for an animal with aquatic respira-

tion. It may be further stated that when the lamprey has gorged itself with blood, the first marked change appearing in the blood taken as food is the reduction of the oxy-hemoglobin to hemoglobin. Without doubt the oxygen stored in the hemoglobin by the respiratory activity of its prey is used for respiratory purposes by the lamprey. As pointed out by Bert ('70) and others, any thin and highly vascular membrane may serve as a respiratory membrane. The alimentary canal of the lamprey answers admirably these conditions, and on opening the gorged intestine of a lamprey just taken from a fish, one can trace with the eye alone the gradual transformation of the oxygenated blood through gradually darkening shades until the blood is almost black. Examined with the micro-spectroscope, the transformation can be followed with great definiteness and by agitating the black blood with air it reddens and the two characteristic bands of oxy-hemoglobin reappear. No doubt this use of the oxygen obtained by another fish is of considerable importance to the lamprey, and there is realized by it very perfectly the obtaining of ordinary and gaseous food at the same time.

With the larva, the motions are very energetic for a short time, then the animal lies on its side panting, as it were, the respirations are so rapid. In nature, however, only very rarely is great exertion necessary, as in burying itself in sand after voluntarily or accidentally becoming free in the water, also by moving through the sand for a more favorable locality. Almost the only other muscular activity consists, not in moving the whole body, but in pumping water into and out of the broncho-œsophageal chamber for the combined purpose of respiration and obtaining food.

Respiratory Mechanism and Movements in the Larva.—If a larval lamprey is placed in a glass vessel with coarse sand and a plentiful supply of water it will very soon make a suitable burrow or canal in which to live. Very frequently the burrow will be made in part next to the glass, in which case one may observe with great definiteness all the respiratory movements, especially if a magnifier is used. It is seen that in repose the respirations are not far from 100 per minute, sometimes

less, often many more. If the head is exposed and there are any particles in the water a constant stream is seen to flow into the mouth. Only when the respirations are very slow is the stream into the mouth intermittent.

As the burrow is ordinarily open, as shown in Pl. VIII, Fig. 49, some particles of corn starch dropped into it diffuse in the water and one can then see the direction of the stream from the particles of starch. Starch is the most satisfactory substance used with the larval lampreys as they are not irritated by it. In fact it is taken into the alimentary canal. In case the water contains minute filaments these will often be drawn by the stream to the mouth, but the sieve or net work formed by the oral tentacles catches them and prevents their entrance into the respiratory chamber. Whenever the oral sieve becomes at all clogged by adhering particles, the current is reversed and the offending débris washed off most energetically. If attention is directed to the branchiopores or gill openings, it is seen that, with every constriction, streams of water shoot out obliquely caudad. The valves over the branchiopores (Pl. VIII, Fig. 52, *vl.*) project outward, but as soon as the branchial apparatus expands for inspiration the valve closes the branchiopore so that water does not enter it, and thus all the water entering the gill cavities must enter through the mouth. It is seen also that while the stream into the mouth is practically continuous, its exit through the branchiopores is intermittent.

If a larva is placed in a dish of water it swims around somewhat aimlessly but rapidly for a time, but finally rests on its side. The side on which it lies seems to be a matter of indifference, and is therefore sometimes the right and sometimes the left. If the water in the vessel is not too deep, the current made by the jets of water from the branchiopores is easily demonstrated by putting bits of wood or cork on the water over the gill-openings. They follow the current almost directly caudad along the whole length of the larva. If the position of the larva is noted, and then it is observed again after 15 or 20 minutes it is seen that it has moved cephalad or forward due to the recoil or reaction of the jets of water forced

from the gills. The forward movement is not so great, however, as might be expected from the strength of the backward current, and the slight retardation due to the friction of the bottom of the vessel. While the animal is lying on its side, the current into the mouth is clearly seen by dropping a little starch into the water. The currents can also be very satisfactorily studied by placing the animal in a test-tube or narrow jar with water and a little corn starch.

Whenever the head of the larval lamprey can be seen in a good light, an arched, reddish, moving body is visible through the translucent body wall between the opening of the mouth and first gill. This is in rhythmical motion toward and away from the mouth. It is the *velum*, composed of two symmetrically placed, arched curtains which perform the double function of valve to prevent the water from going out through the mouth when the branchial apparatus is constricted, and also of moving by its own musculature something as the diaphragm of a mammal and thus alternately increasing and diminishing the size of the branchial cavity. If the movement is carefully watched and compared with the alternate constriction and expansion of the branchial apparatus, it is seen that the expansion of the branchial apparatus and the cephalic or forward movement of the velum coincide, both thus acting to increase the size of the branchial chamber and therefore to draw water into the branchial cavity, that is, both are inspirators. On the other hand, in expiration the velum is drawn caudad at the same time that the branchial chamber is constricted and thus a double diminution of the capacity of the branchial chamber results and the expiration is complete. This caudal movement of the velum has also tended to draw water into the space between the velum and the sieve like tentacles. This water is drawn into the branchial chamber immediately upon the expansion of the branchial chamber and the forward movement of the velum. Owing to the valves over the branchiopores, the branchial chamber can only be filled through the mouth, and a current is drawn into the mouth both in expiration by the caudally moving velum, and in inspiration by the expanding branchial chamber, hence it

follows that the current going in at the mouth must be constant, unless the respiratory movements are exceedingly slow. The reason why the cephalically moving velum does not force the water out of the mouth in narrowing the space between the sieve and the velum is that, as the velum moves forward, it leaves an equal space behind it and thus aspiration is produced in the branchial chamber, and as there is nothing to support the thin mesal edges of the velar folds, they move laterally and thus make a free passage for the water to the branchial chamber, so that the action of the velum alone tends constantly to aspirate the water into the mouth. When the velum is aided by the expanding branchial chamber in inspiration, an increased aspiration is insured and so much the more is there a constant inflowing current.

By careful experiment on transforming larvæ it was found that they continued to take a constant current into the mouth even after they were able to attach themselves to the sides of the vessel containing them by the almost completely developed sucking disc. Those experimented upon buried themselves in the sand and gravel whenever they were given opportunity ; it is believed therefore, that until the young lamprey is entirely transformed and swims freely in the water or becomes attached to a fish, water is inspired through the mouth as well as through the branchiopores, but, in expiration, it passes out only through the branchiopores, except when the branchial apparatus is being cleared of particles taken in with the respiratory currents. The action of the velum may be most perfectly shown by thoroughly etherizing a larva and then carefully removing the ventral body wall between the velum and tentacles so that the velum may be very clearly seen. If now the animal is set up endwise in water one can study very satisfactorily the action of the velar folds. By adding ether occasionally one can control the rapidity of the respiratory movements so that they may be slow enough for careful study. For some purposes one may advantageously remove the entire head cephalad of the velum.

On a frontal section at the level of the branchiopores like the one shown in Pl. VIII, fig. 52, one can very readily see

the course of the water in its passage through the branchial apparatus.

With larvæ in confinement, whenever the water is insufficiently aerated, the head and sometimes the whole branchial apparatus is projected from the burrow into the water. If the water is changed they disappear in a short time. If the water is not changed or aerated in some way the larva will leave its burrow entirely and make violent efforts to escape from the vessel. If one watches the indications he soon learns about how often to change the water ; in any case he knows that the water must be aerated or changed whenever the larvæ give this sign of beginning suffocation.

Respiratory Mechanism in the Adult. — On the change from the larval to the adult form, the food changes from minute organisms filtered from the water to blood sucked from other fishes, and the mode of inspiration must necessarily change ; for when the lamprey is attached for the purpose of obtaining food or for any other object, there is no possibility of inspiring water through the mouth. When unattached, however, water may still be taken into the branchial cavity through the mouth. For a considerable time during transformation and even when the tongue and the mouth have nearly assumed the mature condition, if one watches the particles in the water it is seen that there is still an almost constant stream flowing into the mouth. Later, however, although water may enter the mouth in respiration, it does so rarely, but on the contrary both inspiratory and expiratory streams must pass in and out of the branchial chamber through the branchiopores.

As shown in figure 52 of Pl. VIII, the branchiæ of the larva appear to project freely into a common branchial chamber, although there are seven openings on each side from this chamber. In the adult, on the other hand, there are seven gill pouches on each side, each pouch being independent except for a small opening into the greatly constricted bronchus ; and, as stated above, the respiratory streams are both in and out of each branchiopore so that if the bronchus were entirely occluded and part of the gill pouches obliterated,

as sometimes happens, the respiration of the animal could still be carried on. In other words having 14 practically independent gill pouches renders the liability to suffocation far less than if a single entrance or exit served for the entire respiratory supply.

Since in the adult, the inspiratory stream must enter the same opening from which the expiratory stream emerges, there must be a different arrangement of valves from that obtaining in the larva, where the branchiopores serve only for the exit of the water. The single valve of the larva is present in the adult, but it is not wide enough to cover the entire branchiopore as in the larva ; usually it covers only about the cephalic half (Pl. VIII, fig. 55).

Inspiration is effected largely in both adult and larva by the elasticity of the cartilaginous branchial basket-work, and expiration through the constriction of the branchial apparatus by muscular action, thus standing in marked contrast to the respiratory actions of mammals where the thoracic cage must be expanded by active muscular contraction for inspiration, while expiration is largely effected by the elasticity of the respiratory apparatus.

In the case of the lamprey one might think at first that no valves are necessary in respiration, for if the branchial pouches are open to the surrounding medium through the branchiopores any enlargement of the branchial space would cause the water to enter, and conversely, any constriction would empty the branchial sacs. This view is correct, but this mode of simply drawing water into a sac and expelling it has not apparently answered the requirements of the lamprey, and there is present the thin valve (the ectal valve) which covers the entire branchiopore in the larva (fig. 52–55), and in addition a double valve (ental valve) (fig. 55), which is formed by the growth and modification of the middle gill lamella of the caudal half of the branchial sac. This lamella, near the branchiopore, bifurcates and soon loses its secondary laminæ and each part extends laterad as a firm but flexible membrane attached to the caudal wall of the branchial sac, one to the dorsal the other to the ventral edge of the branchiopore and

also somewhat to the dorsal and ventral parts of the ectal valve. The other or the cephalic edge of each valve is free.

The action of the valves is as follows: In inspiration, the two parts of the inner or ental valve turn away from each other and are pressed toward the cephalic wall of the branchiopore across the channel at the edge of the branchial sac, and the ectal or transverse valve folds over the ental one. By the expansion of the branchial apparatus, the entrance to the gill sac has been rendered more direct and the inflowing stream flows directly into the sac (Fig. 53). In expiration, the water flows through the branchial lamellæ, while around the edges, *i. e.*, at the dorso- and ventro-lateral edges of the gill sac there is formed a canal or gutter by the shortening of the gill lamellæ. The free ends of the lamellæ are also membranous and curved and aid in making a very complete and smooth canal. The ental valves at the entrance to the branchiopore cross this canal and serve as a guide to the inspiratory stream, not allowing the water to get into the canal around the edges of the gill sac, but directing it into the gill sac itself (Fig. 53). In expiration, however, with the change in obliquity and the constriction of the gill sac, the water passes between the branchial lamellæ into the canal and meeting the ental valve rotates the two folds of the valve toward each other and against the caudal wall of the branchiopore, thus removing the obstruction in the canal and really extending it by means of the arched valves (Pl. VIII, Fig. 54, 55). From this arrangement it is seen that two distinct objects are attained, the water not only bathes the gills but passes between the lamellæ, it is then concentrated in a canal with smooth sides where the friction is at a minimum; and in its exit from the branchial sac in expiration, the valves prevent the used water from making a circle in the gills, and more important, they form a very oblique channel which directs the expiratory stream caudad, thus insuring the animal against using the same water over and over. In inspiration, on the other hand, from the direction of the opening, the water enters at nearly a right angle to the axis of the animal, and thus fresh or unrespired water is constantly supplied to the gills. (See figures 51–55, Pl. VIII).

While the branchial pouches are, as stated above, practically independent, nevertheless they do communicate through the common bronchus, and occasionally a particle entering the branchiopore of one side may be seen to emerge from the opposite branchiopore (Bert, '67). If one observes the respiration of a lamprey resting upon its side in very shallow water so that the branchiopores are near the surface, the oblique streams from the branchiopores are very readily seen. If the nostril is near the surface of the water a stream is seen to emerge from it at every expiration. Hence as the nasal sac is closed caudally, a stream must be drawn in at every inspiration and expelled at every expiration. This movement simply accompanies respiration and is not for respiratory, but rather for olfactory purposes. That there is no connection between the stream forced from the nostril and the respiratory water may be easily proved by raising the head slightly above the water. After the first expiration no further jets of water are sent from the nostril until the head is again submerged, thus showing that the water enters and emerges from the same opening.

All the respiratory movements may be artificially imitated on a lamprey soon after death, if the branchial apparatus remains expanded. To insure this the lamprey may be curarized; the branchial apparatus being unconstricted by the paralyzed muscles, expands by its own elasticity, and the animal will die in the inspiratory phase. If now the branchial apparatus is grasped by the hand the expiration may be imitated by constricting the apparatus and the streams from the branchiopores and from the nostril demonstrated. Upon relaxing the grasp the branchial apparatus re-expands and refills the gill pouches. By proceeding slowly, one can see with the greatest accuracy the movement of the branchioporic valves, and what is obscure, from the rapidity of action in the living state, becomes clear and intelligible.

THE BLOOD AND ITS FIBRIN, HEMAGLOBIN AND CORPUSCLES.

As in the higher vertebrates, the blood of the lamprey in all stages, except the very early embryonic ones is red in color

and contains both red and white corpuscles. This blood coagulates very quickly, and the fibrin is composed of exceedingly fine and also coarser filaments. If preparations of lamprey and human fibrin filaments are compared (Pl. VIII, fig. 44, 45), it will be seen that in both there are centers from which these filaments seem to radiate, and that in the lamprey, while there are coarse filaments, the ultimate net-work is almost inconceivably fine and that in order to define it well, homogeneous immersion objectives are necessary. On the other hand the net work of filaments in human and other mammalian fibrin is coarse. This condition has been found in all the mammalian fibrin examined, while the fine network seems to be characteristic of the cold-blooded animals.

The time required for coagulation in the lamprey is short, shorter than for mammalian blood but not nearly so short as for amphibian blood (Gage '90).

The hemaglobin of the lamprey is exceedingly difficult to obtain in crystalline form. The only successful efforts so far have been by using a considerable quantity of blood and adding at the edge of the cover a small amount of a 10 per cent. aqueous solution of pyrogallic acid. The cover is then sealed and put in the light in a cool place. After several days, in successful preparations, crystals appear in beautiful rosettes with frond-like rays radiating from the center.

The Red and White Blood Corpuscles.—It is to the solid constituents of the blood that the greatest interest attaches, and especially to the red-corpuscles; for "as the red blood-corpuscles of the camelidæ form an exception in the great mammalian group in being oval instead of circular in outline, and, according to Gulliver in not forming distinct rouleaux, or rolls, so the red corpuscles of the lamprey eels form an exception in the great non-mammalian group of vertebrates (birds, reptiles, and fishes) in being *bi-concave* and *circular*, instead of *oval* and *bi-convex*, like those of all other animals in this great group. The corpuscles also agree with those of mammals in forming distinct rouleaux. This is most marked in the brook lamprey and the larva. In the 9 mm. embryo the corpuscles were often seen in rolls of three or four in the

circulating blood (Pl. VIII, fig. 42, E. F.). Rouleaux have also been observed in the vessels of a living dog's mesentery. A nucleus is present in all the corpuscles, but as it is small and placed in the thickest part of the corpuscle, it is not apparent in the perfectly fresh ones, except faintly in some of those of the 9 mm. embryo. The corpuscles when fresh appear, therefore, almost exactly like those of man." So complete is the resemblance, that skilled observers have frequently been confused, and pronounced fresh preparations of lamprey's blood to be mammalian. As seen in the table, however, the number of the white corpuscles is proportionally very much greater than in mammalian blood, and the white corpuscles are almost always smaller than the red ones, thus standing in these two particulars in marked contrast with mammalian blood. Furthermore "no element of uncertainty should arise with respect to them in legal medicine, for (*a*), the presence of a nucleus may be readily demonstrated, as it is made apparent by drying, by acetic acid, and by the reagents most used in examining blood for medico-legal purposes; (*b*), except in the embryo 9–10 mm. long, the corpuscles are nearly twice as large as those of man. (Compare the accompanying table of measurements). Hence the red blood corpuscles of lamprey eels, in spite of their bi-concave form and circular outline, really offer no more difficulty in medical jurisprudence than do the corpuscles of any other of the non-mammalian vertebrates.*

"The circular outline of the red blood-corpuscles in both adult and larval lampreys was discovered by R. Wagner and the fact published in 1838 ('38). The bi-concave character is remarked upon by Wagner, Kölliker, and others, but I have seen no reference to the fact that the corpuscles form distinct rouleaux like those of mammals. This feature, as in mammals, is lost soon after death.

"Although the bi-concave character of the corpuscles of lampreys is as easily demonstrated as in the corpuscles of

* While it is true that the red corpuscles of mammalian embryos and the developing corpuscles in the adult are nucleated, the size and uniformly nucleated condition of the corpuscles of the lamprey would sufficiently characterize them.

mammals, it is stated by Gulliver and Günther that they are flat or bi-convex, and Gegenbauer in his Comparative Anatomy, states that the red blood-corpuscles of birds, reptiles, amphibia, and fishes are bi-convex, no exception being made for the lampreys. Parker in his translation of Wiedersheim's Comparative Anatomy of the Vertebrates, says: 'In case of the red corpuscles, the nucleus persists, and the whole cell is bi-convex in all vertebrates below mammals.' In 1887 wide circulation was given to a statement by Shipley ('87), and Thompson ('87), that the red blood-corpuscles of larval lampreys were oval in outline, like the rest of the non-mammalian vertebrates."

And Thompson further adds: "The noteworthy point now is, that myxine possesses red corpuscles similar to those, not of the adult, but of the larval lamprey, which in many ways it resembles otherwise." On consulting the original article by Shipley ('87), the statement is found to be: "The blood corpuscles are of only one kind, large oval disc-like structures, with a well-marked nucleus." The size of the embryo is not given, but it was in the stage before the white blood-corpuscles appear. As all observers have noted the tendency of the red corpuscles to become deformed, one can readily understand that, if the form were observed in sections, from mutual compression the corpuscles would not remain of circular form. If Dr. Shipley examined these corpuscles in the serum of the larva and in the living condition, and they were found oval instead of circular, the fact would be exceedingly interesting and perhaps suggestive. One would hardly expect to find embryonic blood-corpuscles oval, for even in animals in which the red corpuscles of the adult possess an extreme elliptical form the embryonic ones are either circular or approximately so (Kölliker '84. Milne-Edwards).

"That the red blood-corpuscles of both the adult and larval lampreys are circular, bi-concave, nucleated discs, as here described and figured, was repeatedly demonstrated in larvæ from 9 to 142 mm. long, and in numerous adults. In every specimen examined all the corpuscles not irregular were circular in outline. To make sure that this appearance was not

due to reagents, the corpuscles were examined in the serum of the blood, without the addition of any reagent whatever, and to avoid any possible error on account of the small amount of blood in the 9 mm. embryo, the circulating blood was examined. All the examinations were made with a 2 mm. apochromatic objective and an ocular × 12 " (Gage '88).

Table showing the diameter and thickness of the red and of the white blood-corpuscles of the lamprey in the adult and larval condition; also the relative number of red and white corpuscles, and the number of red corpuscles in a cubic millimeter of blood.

	DIAMETER. *Red.*			Thickness.	Ratio of thickness to diameter	Ratio of white to red corpuscles.	No. of red corpuscles in a cubic millimeter.
	Maximum.	Minimum.	Average.				
Lake lamprey (June),	16.16μ	10.1 μ	14.2 μ	5.05μ	1 : 2.8	Male, 1 : 20 Fem., 1 : 15	Male, 391,333 Fem. 334,666
Lake lamprey (Oct.),	16.25μ	10.62μ	13.9 μ	5.0 μ	1 : 2.78	Male, 1 : 17	Male, 513,280
Brook lamprey (May),	15.15μ	10.1 μ	13. μ	5.02μ	1 : 2.59	1 : 95	500,000
Larval lamprey, 142 mm. long,	15.65μ	12.12μ	13.4 μ	3.48μ	1 : 3.8	1 : {4 / 30}	712,950
Embryo lamprey, 9 mm. long,	8. μ	7. μ	7.448μ	1.96μ	1 : 3.8	1 : 10	Not determined.
	White.						
Larval lamprey, 58 mm. long,			5.56μ				
Lake lamprey (Apr.),			7.8 μ				

The blood for measurement and counting was taken from the heart of an animal just killed or from a pithing wound, and mounted without the addition of any liquid. The cover-glass was supported by a hair and sealed with castor oil. Only undistorted corpuscles were measured. The averages were obtained from twenty-five measurements in each case. All measurements were made with a $\frac{1}{12}$ or $\frac{1}{16}$ homogeneous objective, and a Jackson ocular micrometer, the valuation of which was determined by using a Rogers' standard stage micrometer.

In a larva 73 mm. long, the average diameter was 12.44μ—that is, 0.96μ smaller than in the larva of 142 mm. given in the table. Gulliver ('62–'75, p. 845) states that there is little difference between the blood-corpuscles of *Petromyzon planeri*, *P. fluviatilis*, and *Ammocœtes branchialis* [the larval form]; that one description may serve for all three of them; and gives the following measurements: Diameter of the red corpuscles, 11.9 μ; thickness, 4.09 μ; diameter of nucleus, 3.96 μ. Kölliker gives 11.3 μ as the size, not mentioning the species or the age. Welcker ('63), gives 15 μ as the average size of the red corpuscles of *Petromyzon marinus*, with a maximum of 16 μ and a minimum of 13.4 μ. Thickness of the corpuscles, 3 μ. For the larva the average is 11.7 μ, with a maximum of 12.4 μ and a minimum of 10.9 μ. Thompson ('87), gives the size of the red corpuscles of *Petromyzon marinus* as 13 μ to 14 μ. Welcker gives the number of red corpuscles in a cubic millimetre of the blood of *P. marinus* as 133,000.

In my own studies, which have extended through several years and have considered specimens at various seasons, the statements of Gulliver are not wholly verified. On the other hand, as shown in the table, the red corpuscles increase in size with the increase in size of the whole animal. This is most marked in larval life. After nearly reaching their full growth as larvæ the increase of the red corpuscles to the fully adult condition is only about one micron (1 μ), while between the 9 mm. and the 73 mm. larva there is a difference of 5 μ. but only about 1 μ. between the 73 mm. larva and the one 142 mm. long. This fact of the growth in size of the corpuscles with the growth in the size of the body is again in marked contrast with what is known of the mammalian red corpuscles, which in the new born and the fully matured differ very little in size.

The relative number of red and white corpuscles has been determined at various seasons of the year, and while the number of white ones is greater in some specimens than in others, the season does not seem to affect this ratio very markedly. In general, the lake lamprey has a greater relative number of white ones than the brook lamprey, and in the larva they are more numerous than in the adult. In no case was there seen

the proportion given by Thompson, *i. e.*, three or four white ones to one red one. In my own observations the red ones were always in excess of the white ones. (See table above).

The amœboid movements of the white ones are striking and vigorous in both larva and adult, but as a rule the motion does not begin immediately after the preparation is made. It is usually at its greatest about half an hour after the blood is obtained.

SUMMARY AND GENERAL CONCLUSION.

1. Two species of lampreys inhabit the chain of lakes in western New York.

2. One, the brook lamprey (*Petromyzon* or *Ammocœtes branchialis*) is small in size, few in numbers and short-lived, in the adult stage. It is not known in North America outside the Mississippi Valley except in the Cayuga Lake basin. It is probably widely distributed, but from its small numbers and inconspicuous coloring, it has been overlooked (Plate IV, pp. 436, 452).

3. The other, the lake lamprey *Petromyzon unicolor* or *dorsatus*), is of large size, is in great numbers and lives a parasitic life in the lakes for a period of two to three and one-half years, and perhaps longer (Plate I, III, pp. 431, 445, 452).

4. The lake lamprey from the structure and arrangement of its teeth is hardly to be distinguished from the true anadromous sea lamprey, but judged by the physiological test of natural interbreeding it must be considered as specifically distinct (Plate VI, p. 426).

5. Both species have a larval stage and a metamorphosis at the end of from two to four years. Thus agreeing with the Petromyzontidæ wherever thoroughly studied (Plate III, IV, VI, VIII, pp. 449, 452).

6. The proportions of parts of the body with the two sexes of the lake lamprey, are very unlike and mutually interchange between the ordinary non-breeding and the breeding season. (See Table and p. 431).

7. In both species there are striking atrophies and hypertrophies at the spawning season (Plate III, IV, VII, p. 438).

8. Both species construct similar nests for the deposit and

protection of the ova. The larvæ hatch in these nests, remain there till they are about 12 to 15 millimeters in length, then they seek a sand bank in the concavity of the stream. In this bank they remain until fully transformed and supplied with horny teeth. They then leave the sandy covering and lead a roving, parasitic life in the open waters of the lake (Plate VII, VIII, pp. 441, 449).

9. In its larval life the lamprey is not injurious to man, but aids him by serving as bait for food fishes (p. 457).

10. During adult life the lamprey is highly injurious, as it preys upon food fishes. The lake lamprey is the more injurious from its larger size, greater numbers and longer parasitic life (pp. 445, 457).

11. The lakes could be easily freed from lampreys, by catching and destroying them when they are on their way to the spawning grounds up the lake inlets (p. 461).

12. The respiratory mechanism of the lamprey is very perfect at all stages. From the perfection and arrangement of the branchial valves, the expired water is not re-inspired (Plate VIII, pp. 463, 467).

13. The blood-corpuscles are of two kinds, white and red as in most other vertebrates.

14. The white blood-corpuscles are relatively more numerous than in mammalian blood; they are mostly smaller than the red blood-corpuscles and exhibit active amœboid movements (Plate VIII. p. 471).

15. The red blood-corpuscles are bi-concave, circular discs as with mammalian blood-corpuscles, and like the mammalian red blood-corpuscles those of the lamprey arrange themselves in rolls or rouleaux, (Plate VIII, p. 472).

It is assumed throughout this paper that the lake lamprey is a land-locked species which is a recent offshoot from the true anadromous sea lamprey. But for the very striking similarity, a similarity amounting almost to specific identity with the sea lamprey, one might be strongly inclined to the belief that the lake lamprey is an original product of the lake waters and has only a remote relationship with the sea lamprey through some primitive and common ancestor. On the other hand it might be urged that as there is free communication between

the lakes and the ocean through the St. Lawrence River, there is no occasion to consider the lake lamprey as a land-locked form at all.*

While it is true that the natural obstacles are not such as to prevent the immature lampreys from passing to the ocean and then returning when mature to deposit their spawn, the distance inland is greater than undoubted sea lampreys have ever been known to pass; certainly none have ever been found in Cayuga and Seneca lakes by the writer, and from information obtainable from others none have been seen in any of the lakes or in Lake Ontario.†

The final and definite proof that the lake lampreys remain permanently in the lakes and do not go to the ocean at any time, has been abundantly obtained during the past 18 years by the capture of examples of the adult form of all sizes in the waters of the lake during every month of the year, while the true anadromous forms are found in the inland waters they are known to inhabit, only when very small and when spawning.

As to a reasonable hypothesis for the presence of these isolated or land-locked lampreys: It is recognized by all modern geologists and physical geographers that the present contour of the country and the details of the topography of the greater and lesser lake basins with their water courses and ridges are, geologically speaking, only of recent date. By glancing again at the small topographical map (Pl. II) it can readily be seen that during the glacial epoch when the basins of the St. Lawrence and of the lakes were filled with ice, the water from the melting ice accumulated and finally passed the low elevation south of the lake basin and found its way to the Susquehanna River. Later, as the ice sheet receded, the outlet was through the Mohawk into the Hudson River. Finally

* The common eel (*Anguilla rostrata*) is also abundant in the lakes. As it has been determined by recent investigations that the common eel goes to the ocean or to brackish water to spawn and the young return to fresh water to mature, it will be seen that the passage to and from the ocean is not insuperable.

† I wish to express my indebtedness to the State Game and Fish Protectors who so fully and courteously answered the questions concerning the lampreys of their respective districts.

as the ice melted the superfluous water of all the lakes gradually found an exit through the St. Lawrence basin as it had done in pre-glacial times.

The application of these geological or topographical changes would have the following bearing upon the special subject of this paper. At the present time in the Susquehanna River, only a few miles to the south of Cayuga Lake, the large sea lampreys are found in the summer or spawning season and the transforming ones in the autumn, and larvæ during the entire year, thus showing that even at the present day the large sea lamprey uses the Susquehanna for a spawning ground. The same is true of the Hudson River.

Now it is believed that while the lakes poured their superfluous waters southward into the Susquehanna River that the large sea lampreys frequented the lake and its tributaries and found suitable spawning grounds. As the glacier receded and the streams draining the lake into the Susquehanna became shallower and more difficult to ascend and descend, the lakes were less and less and finally no more visited by the spawning lampreys; and some of the newly transformed ones, finding abundant food in the common fishes which swarmed in the waters, remained and matured in the lakes, and spawned in its tributaries thus completing the entire life-cycle in fresh water.

It is also possible that as the water courses to the Susquehanna decreased and those to the Mohawk and Hudson increased, the lampreys entered and left the lake through those streams, but ultimately the same result would follow and the forms become isolated in the lakes.

If it is granted that the presence of the lake lampreys can be satisfactorily accounted for in the way described, it is not difficult to conceive of the diminiution in size and perhaps also of the other modifications, as the great increase of the dorsal ridge in the male; for it is within human observation that sea animals that have been artificially or naturally isolated from the ocean gradually decrease in size, and that special features may become accentuated or intensified.

Ithaca, N. Y.
September, 1893.

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'82. JORDAN, D. S. and GILBERT, C. H. Synopsis of the fishes of North America. Bulletin of the U. S. National Museum, No. 16, pp. 1018. Good references to systematic literature.

'85. —— and FORDICE, M. W. A review of the North American Species of Petromyzontidæ, with an additional note on the Lampreys of Cayuga Lake, by S. E. Meek. Reprint, pp. 279–296. (Place and periodical in which published not indicated on reprint). On p. 284 the authors say of the lake lamprey: "The characters assumed to distinguish this form from the true marinus are, however, more or less inconstant and not of specific value." Very full references to systematic literature.

'87. JULIN, C. Recherches sur l'anatomie de l'ammocœtes. Bulletin scientifique du department du nord. 2d ser., X, 42 pp.

'90. KÆNSCHE, C. C. Beiträge zur Kentniss der Metamorphose des *Ammocœtes branchialis* in Petromyzon. Schneider's Zoologische Beiträge. Band II, Heft II, pp. 219–250. The author believes that the oral tentacles disappear, except the ventral median one which is transformed into the adult tongue.

'84. KÖLLIKER, A. Grundriss der Entwickelungsgeschichte. 8°, pp. viii+454. Leipzig. On p. 63 it is stated that the red blood corpuscles of the chick are, in the course of development, at first circular.

'90. KUPFFER, C. Die Entwickelung von *Petromyzon Planeri*. Arch. f. mikr Anat., XXXV, pp. 469–558.

'82. LEGOUIS, P. S. Recherches sur le pancréas des cyclostomes et sur le foie dénué de canal excréteur du *Petromyzon marinus*. Compt. Rend. Acad. des Sci. Paris, XCV, pp. 305–308.

'73. LANGERHANS, P. Untersuchungen über *Petromyzon planeri*. 8°, 114 pages. Freiburg. The histology of many of the organs is given.

'35. MAYER. Analecten für vergleichende Anatomie, I Theil, p. 60. This has not been seen, but it is referred to by Schneider and others for observations upon respiration and the respiratory organs.

'88. MEEK, S. E. Notes on the fishes of Cayuga Lake basin. Annals of the New York Acad. of Sci., IV, pp. 297–316. See also Gage and Meek above ('86).

'89. —— Note on *Ammocœtes branchialis*. Amer. Nat. XXIII, pp. 640–642.

'57–'58. MILNE-EDWARDS. Leçons sur la physiologie et l'anatomie de l'homme et des animaux. 8°, 14 vols., Paris 1857–1880. Very excellent bibliography in volume 2, (1857) pp. 246–247, 256–257 and in volume 3 (1858) p. 370.

'71. MILNER, J. W. Report of the fisheries of the Great Lakes; the result of inquiries prosecuted in 1871–1872. In the report of the United States Fish Commissioner for 1872–1873. In discussing the sturgeon fishery Mr. Milner says they frequently have raw sores upon them due to the lampreys. He thinks the lampreys eat the slime of the sturgeon.

'92. MINOT, C. S. Human Embryology. 8°, pp. 815. New York.

'56. MÜLLER, A. Ueber die Entwickelung der Neunaugen; ein vorläufiger Bericht. Archiv f. Anatomie, Physiologie und wissentschaftliche Medicin (Müller's Archiv)., 1856, pp. 323–339. First scientific account of the transformation of larval lampreys into adult Petromyzon. Up to this time the larvæ had been placed in a separate genus (*Ammocœtes branchialis*). But little has been added to Müller's account of the more obvious changes from the egg to the adult lamprey. He reported the presence of an 8th branchiopore in the embryo ("Am Halse befinden sich 8 Visceralspalten, deren vorderste, schon durch ihre Richtung verschieden, sich bald wieder schliesst"). The discovery of an 8th gill opening in the embryo is ascribed to Huxley by Shipley ('87, p. 349).

'43. MÜLLER, J. Untersuchungen über die Eingeweide der Fische. Abhl. d. kgl. Akad. der Wissensch. zu Berlin, 1843, pp. 109–170. Announces (p. 119) that the red blood corpuscles are elliptical in Myxine.

'90. NESTLER, K. Beiträge zur Anatomie und Entwickelungsgeschichte von Petromyzon Planeri. Zool. Anz., XIII, pp. 11–12; Arch. f. Naturgeschichte, 1890; Ann. Mag. Nat. Hist. ser. 6, Vol. v, pp. 262–263. He believes that the œsophagus of the adult develops from a solid cord along the ventral side of the dorsal aorta in the larva. Compare Schneider, ('79, p. 94).

'80. NUSSBAUM, M. Zur Differenzirung des Geschlechts in Thierreich. Arch. f. mikr. Anat. XVIII, pp. 1–121. As eggs of Petromyzon are all at the same stage of development, the author thinks the lampreys die after spawning (p. 47) thus agreeing with A. Müller ('56, p. 334).

'**61**. OWEN, R. Comparative Anatomy and Physiology of vertebrates. 8°, 3 vols., London, 1861–1868. Vol. I., 1861.

'**82–83**. PARKER, W. K. On the skeleton of the marsipobranch fishes, part 2, Petromyzon. Proc. Roy. Soc., 1882, pp. 439–443; 1883, pp. 1–3; Philos. Trans. Roy. Soc. part 2, 1883, pp. 373-457.

'**84**. PARKER, T. J. A course of instruction in Zootomy, Vertebrata. 8°, pp. 397. London and New York. Good account of the anatomy of the adult lamprey.

'**88**. ROLLESTON, G. Forms of animal life, a manual of comparative anatomy with descriptions of selected types. Second edition, revised and enlarged by H. W. Jackson. pp. xxxii + 937. Oxford. "At the metamorphosis the tubular structure [of the liver] is lost; fat appears in the cells; the gall-bladder, and bile duct are absorbed. . . . . The pancreas is perhaps represented in the lampreys by an acinous gland opening into the widened commencement of the mid-gut on the left side" (p. 435).

'**79**. SCHNEIDER, A. Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere. 4°, pp. 164. Berlin. Discusses the habits, structure and transformations of lampreys.

'**81**. SCOTT, W. B. Beiträge zur Entwickelungsgeschichte der Petromyzonten. Morph. Jahrb., VII, pp. 101–172.

'**87**. —— Development of Petromyzon. Jour. Morph., I. pp. 253–310. The myel is rounded in the embryo, flattens before adult life.

'**86**. SEELEY, H. G. The fresh water fishes of Europe; history of their genera, species, structure, habits and distribution. 8°, pp. 444; London, Paris, New York and Melbourne.

'**87**. SHIPLEY, A. E. On some points in the development of *Petromyzon fluviatilis*. Quar. Jour. Micr. Sci., XXVII, pp. 325–370. On p. 343 he says that in the embryo there is but one form of blood-corpuscle and that this is "large, oval and disc like."

'**87**. THOMPSON, D'ARCY, W. On the blood corpuscles of the Cyclostomata. Ann. and Mag. Nat. Hist., Ser. V, Vol. XX, pp. 231–233; Anat. Anz., II, pp. 630–632.

'**38**. WAGNER, R. Beiträge zur vergleichenden Physiologie, Vol. II, 1838. Nachträge zur vergleich. Physiol. des Blutes, p. 13. First announcement that the red blood corpuscles of larval and adult lampreys are circular and biconcave.

'**63**. WELCKER, H. Grösse Zahl, Volum, Oberfläche und Farbe der Blutkörperchen bei Menschen und bei Thiere. Zeit. f. ratl. Med., 3d Reihe, XX, pp. 257–307.

EXPLANATION OF THE PLATES.

Plates I, III, IV, and V are from photographs of fresh or preserved specimens. The specimens in most cases were immersed in water or alcohol, and photographed with a vertical camera. Plates VI, VII, and VIII were drawn by Mrs. Gage from photographs or from the object by the aid of a camera lucida.

PLATE I. FIG. 1–2.

A pair of lake lampreys about 33 centimeters long, from the same nest; obtained June 9, 1893. At the head of the article.

FIG. 1. Male lake lamprey showing dorsal ridge and the approximation of the two dorsal fins. This specimen weighed 101 grams.

FIG. 2. Female lake lamprey. The dorsal fins are not connected, and no dorsal ridge is present, but the anal notch is marked. This female had almost completed spawning, and hence appears slender. Compare with the sea lamprey full of eggs (Fig. 17, Pl. V).

The stone to which the specimen is attached weighed 199 grams, the specimen only 72 grams. While this pair were in the nest and under observation the female was seen to drag this stone down the stream for a considerable distance.

PLATE II. FIG. 3–4.

Map of the head of Cayuga Lake, showing the surrounding country and the streams flowing into the lake. (From W. R. Dudley's Cayuga Flora.) The squares on the map are kilometers and the zero point is the University Signal Station (U. S. S.) point of reference, a point on the University campus, whose latitude and longitude have been determined with great accuracy by the Department of Civil Engineering. Fig. 4, in the upper right hand corner, is a topographical map of the lake basin designed especially to show the lakes and their outlet through the Oswego River, the water-shed around the basin is indicated by interrupted lines, and also the water courses draining the elevation surrounding the lake basin. It is to be noted that the Susquehanna River with its tributaries is the most important of these.

There is an important ridge between Lake Ontario and the interior lake basin, and this elevation is drained by numerous small streams flowing northward into Lake Ontario. It is to be especially noticed also that this elevation is broken through by the Oswego River.

L. Lake; *R.* River; *Cnd.* Canandaigua Lake; *Crkd.* Crooked or Keuka Lake; *Owsc.* Owasco Lake; *Sktls.* Skaneateles Lake; *Ond.* Onondaga Lake. Several small lakes have been omitted.

PLATE III. FIG. 5–10.

Figures to represent the relations of the two dorsal fins in the male lake lamprey in and out of the spawning season, the female in the spawning season, and two larvæ of very different sizes.

FIG. 5. (About $\frac{1}{3}$d natural size). The first lake lamprey obtained. The branchial apparatus is in the inspiratory phase, and therefore widely expanded. The dorsal ridge, so characteristic of the male lake lamprey, is more than usually prominent in this specimen; the fusion of the two dorsal fins is also shown.

FIG. 6. ($\frac{1}{3}$ natural size). Part of a male lake lamprey caught in December, to show the decided interval between the two dorsal fins; also to show the non-appearance of the genital papilla out of the breeding season. The myotomes are also very clearly indicated.

FIG. 7. ($\frac{1}{3}$ natural size). Segment of a male lake lamprey in the spawning season, to show that the two dorsal fins appear continuous or simply notched during this season. The genital papilla is also very prominent at this period.

FIG. 8. ($\frac{1}{3}$ natural size). Caudal end of a female lake lamprey in the spawning season to show the separation of the dorsal fins even in the breeding season in the female; the notched appearance of the vent and the fin-like fold extending to the caudal fin.

FIG. 9. (Natural size). The caudal half of a larval lamprey 150 millimeters in length, to show the separation of the two dorsal fins. The myotomes are also well shown in part of the length.

FIG. 10. (Natural size). A small larval lamprey to show the separation of the dorsal fins even in specimens of this size. In specimens only 40 mm. long, there is a notch in the fin showing plainly where the interval is to be.

PLATE IV. FIG. 11–15.

Brook Lampreys and a larva just before transformation.

FIG. 11–12. (Natural size). A pair of brook lampreys taken at the spawning season. Photographed under water with a vertical camera. The male (Fig. 11), has a somewhat prominent genital papilla. In the female (Fig. 12), there is present a marked anal fin-like fold, and the caudal part of the abdomen is full of eggs. In both male and female there is a notch, but no interval between the two dorsal fins, and in the female the cephalic part of the second dorsal is edematous. Compare figure 14.

FIG. 13. (Natural size). The caudal part of a brook lamprey that had just transformed. The specimen was taken in October, and measured 200 millimeters in length. The two dorsals are widely separated, but appear to be connected by a very low ridge.

FIG. 14. (Natural size). An oblique view of the caudal part of a female brook lamprey especially to show the edematous second dorsal fin, filling, almost completely, the notch between the two dorsals. Near the end of the spawning season this edema is frequently infiltrated with blood so that the females are marked by a bright scarlet spot.

FIG. 15. (Reduced $\frac{1}{10}$th). Larval lamprey, 190 millimeters in length, to show the size the larvae may reach before transformation. This one is longer than the adult brook lampreys here figured, but not quite so long as the one from which figure 13 was taken.

PLATE V. FIG. 16–18.

A pair of sea lampreys, from Lawrence, Mass., running up the Merrimac River to spawn. Photographed under water after preservation in Müller's fluid.

FIG. 16. (About ⅓d natural size). A male sea lamprey 575 millimeters long at the spawning season. The dorsal ridge is very low and the two dorsals are separated by a considerable interval. The eyes were sunken and obscured during the preservation.

FIG. 17. (Somewhat less than ⅓d natural size.) A female sea lamprey 645 millimeters in length at the spawning season. The eggs had not yet been shed, hence the fullness of the abdomen. Opposite the first dorsal fin the roundish white mark indicates the place where another lamprey had attached itself to this one. The incompleteness of the tail on the ventral margin is due to some accident either before or after death.

FIG. 18. (Natural size). Ventral view of the head of the male lamprey shown entire in figure 16. To show the arrangement of the sensory or nerve papillae (see Fig. 20 and 51, Pl. VI and VIII). The circumoral fringe or plaiting and the lateral closure of the mouth are also shown. The oblique direction of the branchiopores is shown, especially on one side.

PLATE VI. FIG. 19-26.

The mouth and its appendages in the adult, transforming and larval stages. The figures of the adult mouths are from photographs of the fresh specimens made during the spawning season. The other figures are from camera lucida drawings of preserved specimens. The magnification of each is given immediately after the number of the figure.

FIG. 19. (× 2). The ventral aspect of the head of a lake lamprey especially to show the arrangement and number of the teeth. By comparing the teeth of the supra- and infra-oral laminae with those of the annular cartilage from another specimen (Fig. 24), it will be seen that there are 9 infra-oral teeth on the annular cartilage, and 8 in Fig. 19. The range is from 6 to 10, the most common number being 7 or 8. In rare cases the two supra-oral teeth are fused, thus giving the appearance of a single median tooth.

E. Eye.

S. O. Sense organs or nerve papillae. For those on the lateral and dorsal aspect of the body, compare figure 51 of plate viii.

FIG. 20. (× 2). Ventral aspect of the head of a sea lamprey from Lawrence, Mass., to show the oral disc with its concentric rows of teeth, the supra- and infra-oral teeth and the teeth of the tongue. Compare figure 25.

S. O. Sensory organs or nerve papillae.

FIG 20. *A-E.* (× 5). Enlarged papillae from the circumoral fringe, to show their size and form at different parts of the circumference. In the lake lamprey the papillae are almost exactly like those here shown, not differing more than the papillae in different sea lampreys.

A-B. From the fringe at the meson and the cephalic edge of the disc.

C-D. Papillae from the side of the disc.

E. Papillae from the meson at the caudal side of the disc.

FIG. 21. (× 3¼). Ventral aspect of the head of a brook lamprey to show the number and arrangement of the teeth. The body opposite the gills is enlarged, as the photograph was taken during the inspiratory phase. The whole dentition is seen to be weak as compared with the lake or sea lamprey. The lingual tooth plate is also markedly different.

E. Eye.

S. O. Sensory organs or nerve papillae.

A–C. (× 12.) At the left. Papillae from the circumoral fringe of the brook lamprey. *A* is from the meson at the cephalic edge, *B* from the side, and *C* from the meson at the caudal edge of the disc.

FIG. 22. (× 16). Ventral view of the head of a larval lamprey 135 millimeters long to show the ventral lip, the upper or dorsal hood-like lip, and the branched tentacles forming a sieve over the entrance to the mouth. In this figure the tentacles are somewhat unnaturally separated. During life they are more closely approximated, thus making a fine strainer to prevent the entrance of coarse particles into the branchial cavity. By comparing with figure 41 of plate vii, the entire tentacle will be seen to resemble a cauliflower somewhat.

D. L. Dorsal lip or hood. It embraces the lateral extensions of the ventral lip.

L. T. The ventral median tentacle which may be designated the *lingual tentacle* as it is supposed to be an important factor in the formation of the adult tongue.

V. L. Ventral lip. Its lateral extensions are entad of the dorsal lip.

FIG. 23. (× 16). Ventral view of the head of a transforming larva, to show the narrowing of the head and mouth at this stage, and also the arrangement of the tentacles around the oral disc, as if they were to be transformed into the future teeth. The union of the dorsal and ventral lips to form the circular, oral disc is also shown.

D. L. and *V. L.* The dorsal and ventral lips in the process of fusing.

L. T. The tongue which appears to be derived largely from the median lingual tentacle. Compare figure 22.

FIG. 24. (× 3). Annular cartilage of a lake lamprey, to show the form of the cartilage and the position of the supra- and infra-oral teeth.

F. Foramen opening into the interior of the cartilage. There is something of an angle at the point of entrance of the foramina and the general appearance is strikingly like the jaws of a shark.

I. L. Infra oral or mandibular teeth. There were nine in this specimen, eight in the one represented in figure 19.

S. L. Supra-oral lamina or maxillary teeth.

FIG. 25. (× 2½). Annular cartilage and part of the tongue with the lingual teeth of a sea lamprey. The tooth plates are removed from the annular cartilage, thus bringing into view the supporting eminences of cartilage for each tooth.

F. Foramen near the middle of the annular cartilage.

I. L. Infra-oral or mandibular tooth supports.

L. T. Lateral lingual teeth. There are thirteen on the right and but ten on the left. Ordinarily the lateral variation is not so marked.

S. L. Supra-oral or maxillary tooth supports.

T. Part of the tongue.

V. L. Ventral lingual lamina. Compare the ventral lingual tooth-plate in figures 19–20, and 21.

FIG. 26. (× 7). Annular cartilage of the brook lamprey.

F. Foramen leading to the interior of the cartilage. Compare the same in figures 24, 25.

I. L. Infra-oral lamina supported by the ventral half of the annular cartilage.

S. L. Supra-oral lamina or maxillary tooth-plate supported by the dorsal half of the annular cartilage. This plate is in marked contrast to those of the lake and sea lamprey, where the maxillary teeth are very close together. Brook lampreys are occasionally found with one or more intermediate teeth on the supra-oral lamina. (Jordan, '82, '85.)

PLATE VII. FIG. 27–41.

A series of transections near the middle of the body to show the changes in the gonads (ovary and spermary) at various stages of growth; atrophy of the intestine in the breeding season; nest building, and the oral tentacles and velar fold of a larva. The scale is indicated after the number of each figure.

Structures appearing in all the transections, all abbreviations on Fig. 27.

A. Aorta.

C. V. Cardinal veins.

G. Gonad. The reproductive gland (ovary in the female, spermary in the male.) *G.* On each section. The ovary and testis are single, foliated organs in the lamprey, and are supported by a fold of peritoneum, Mesogonad, frequently called mesorchium in the male, mesoarium in the female.

I. Intestine. *I.* On all sections.

IM. L. Intermuscular ligaments between the myotomes.

K. Kidney and ureter.

M. Y. Myel, or spinal cord.

M. A. Mesenteric artery.

M. G. Meso Gonad. The duplicature of peritoneum supporting the ovary (*mesoarium*) or spermary (*mesorchium*).

M. P. Muscle plates cut transversely. *M. P.* on Fig. 27, and 36. Each myotome is made up of a multitude of muscle-plates or lamellae, each in a delicate connective tissue sac. Only the empty sacs are shown in the figures.

M. T. Myotome or myomere. These overlap like tiles, so that in a transection of the body the cut ends of several appear. The overlapping myotomes are connected by the intermuscular ligaments (*IM. L.*).

M. V. Mesenteric vein. The mesenteric vein and artery are in the typhlosole.

N. Nucleus. On Fig. 29 A.

NC. Notochord.

T. Typhlosole, or spiral intestinal valve; letter on Fig. 27 and 37. The tissue of the typhlosole appears to be largely lymphoid in character. In the figures of the larva, the typhlosole is shown clearly to be a linear invagination of the intestine, thus forming a ridge. Commencing somewhat cephalad of the base of the left dorsal fin, the typhlosole or spiral valve extends cephalad as a right-spiral, and caudad as a left-spiral.

FIG. 27. (× 2½). Transection of an adult male lake lamprey taken in December, to show the size and appearance of the spermary about six months before the spawning season. The intestine also shows the size and general structure in the feeding specimens.

FIG. 27, *A*. (×53 and 700). A. Sperm mother-cell showing the multitude of sperm-cells within it. *B*, *C*. Individual sperm-cells magnified 700 diameters, to show their structure and appearance. In *B*, from an osmic acid preparation, two black spherules are shown in the darker part. *D*, A red blood-corpuscle with its eccentric nucleus, at the same magnification as *B*, *C*, to show the relative size of sperm-cells and red blood-corpuscles.

FIG. 28. (× 20). Figure of the edge of a lamella or lobule of the spermary, from the same specimen as figure 27, to show the appearance of the sperm mother-cells by reflected light. By comparing with figure

30 one can readily see the difficulty in distinguishing spermary and ovary. When properly prepared and viewed as transparent objects, however, the difference between the sperm mother-cells and the ova is most striking.

FIG. 29. (× 2½). Transection of a female lake lamprey taken in December, *i. e.*, about six months before spawning. To show the size of the ovary and of the intestine; compare description of Fig. 27 and 28.

FIG. 29 A. (× 53). A single ovum from the ovary of the same specimen as figure 29. To show the comparative size and general character of the ovum, with its eccentric nucleus; also to compare with a sperm mother-cell of the same stage of development. Compare Fig. 27 A.

FIG. 30. (× 20). End of a lobule of the ovary of the same specimen as figure 29. To show the general appearance of the ovary and ova about six months before spawning. Also the similarity in appearance of ovary and spermary at this stage of maturity. Compare Fig. 28 with its description.

FIG. 31. (× 2½). Transection of a male lake lamprey in the breeding season, to show the relative size of spermary and intestine, and for comparison with the spawning female (Fig. 32), and the non-spawning male (Fig. 27), also the enormous dorsal ridge appearing in the male lake lamprey during the breeding season.

D. Dorsal ridge.

FIG. 32. (× 2½). Transection of a female lake lamprey in the spawning season. Some of the ova are free. Compare with the non-breeding female (Fig. 29), and the breeding male (Fig. 31). While in the male the spermary is considerably larger at the breeding season, the ovary has far more strikingly increased in size.

FIG. 32 A. (× 53). Ovum of the spawning lake lamprey. The nucleus is obscured by the great amount of food-yolk. This figure is of the same magnification, and is introduced for comparison with figures 29 A, 34 A, 36 A, and 38 A, to show the difference in size of the ovum at various stages of maturity. It is also at the same magnification as the sperm-mother cells shown in fignres 27 A, and 35 A.

FIG. 33. (× 6). Transection of a just transformed male lake lamprey taken in October, and about 150 millimeters in length. To show the size of the spermary and of the intestine, and for comparison with a female at this stage (Fig. 34).

FIG. 34. (× 6). Transection of a just transformed female lake lamprey, about 150 millimeters long, taken in October. To show the ovary and intestine, and for comparison with the male at this stage (Fig. 33), also with the female brook lamprey (Fig. 36).

FIG. 34 A. (× 53). Ovum from the same specimen as figure 34. To show the size of the ovum at the time of transformation, and for comparison with the ovum of a brook lamprey at the same stage (Fig. 36 A), also with a larva (Fig. 38 A).

FIG. 35. (× 6). Transection of a just transformed male brook lamprey, about 190 millimeters long, caught in October. To show the intestine and the spermary, and for comparison with the just transformed female brook lamprey and the lake lamprey at the same stage (Fig. 33, 34). It will be noticed that the intestine is relatively smaller than in the just transformed lake lamprey.

FIG, 35 A. (× 53). Single sperm-mother cell of the just transformed brook lamprey, from the same specimen as figure 35.

FIG, 36. (× 6). Transection of a female brook lamprey, about 190 millimeters in length. Just transformed ; caught in October. For comparison with the male (Fig. 35), and with the female lake lamprey at the same stage (Fig. 34). It will be seen that the brook lamprey's ovary is much nearer maturity than is that of the just transformed lake lamprey.

FIG. 36 A. (× 53). Ovum from the ovary of the same specimen as figure 36. To show the size of the ovum in the just transformed brook lamprey, and for comparison with the lake lamprey (Fig. 34 A). It will be seen that this ovum is even larger than the one from the ovary of a lake lamprey six months before spawning (Fig. 29 A). From the appearance of sexual maturity it is believed that the brook lamprey spawns the spring following its transformation.

FIG. 37. (× 6). Transection of a larval male lamprey, 140 millimeters long ; caught in November. To show the small spermary and the intestine with a crescent-shaped lumen, due to the intruding typhlosole or valve ; no secondary folds are present as in the adult.

FIG. 38. (× 6). Transection of a larval female lamprey, 150 millimeters long ; taken in November. To show the ovary with the ova and the intestine. It was not cut at the same level as figure 37, hence the spiral valve or typhlosole occupies a different position.

FIG. 38 A. (× 53). Ovum from the ovary of the same specimen as figure 38.

FIG. 39. Section of a lake lamprey's nest with a pair of lampreys. The nest is sectioned parallel with the stream ; it is represented in the usual place for a lamprey's nest, just above ripples.

The female lamprey is represented as moored to a large stone, while the male is backing down stream carrying a stone of considerable size. It will be readily seen that disturbance of the stones at the upper edge of the nest would loosen the sand, and that it would be washed down stream and thus tend to fill the bottom of the nest, as shown. Mingled with the sand at the bottom of the nest are seen numerous ova, indicated by white circles.

FIG. 40. Face view of a creek with two lamprey nests just above ripples. In one nest two lampreys are indicated and in the other but one. In the concavity of the stream, where the water flows somewhat slowly, there is shown a deposite of sand and mud. It is in such situations that the larvæ live after leaving the nest.

FIG. 41. (× 8). A medisection or median sagittal section of a larval lamprey, 135 millimeters long. To show the oral tentacles, one side of the velum, and the relation of the velum to the branchial chamber. To be compared with the frontal section shown in figure 52, Plate VIII.

B. R. Branchiæ. They occupy a common chamber. The B. R. is on the third gill.

D. L. Dorsal lip or hood. Nearly its entire substance is muscular.

N. Single nasal opening.

N. C. Notochord.

V. L. Ventral lip.

VELUM. The right half or fold of the velum. There is a similar one in the left half of the body. Compare with figure 52 of Plate VIII.

PLATE VIII.

FIG. 42. (× about 1000). Red Blood-Corpuscles of lake, brook and larval lampreys. (From the *New York Medical Journal*).

A. Red blood-corpuscles of the lake lamprey. *a*, face view of a corpuscle; *b*, optical section of a corpuscle on edge; *c*, face view of a corpuscle, showing the nucleus after the action of one per cent. acetic acid; *d*, cup-shaped corpuscle.

B. Red blood-corpuscles of the brook lamprey. *a*, *b*, *c*, the same as in *A*.

C. Red blood-corpuscles of a larval lamprey 142 mm. long. *a*, *b*, *c*, as in *A*.

D. Red blood-corpuscles of a larval or embryo lamprey, 9 mm. long. *a*, *b*, *c*, the same as in *A*.

E. Rouleaux of the corpuscles of the brook lamprey in optical section. In the lower corpuscle a nucleus is indicated to show that it is small and in the thickest part of the corpuscle. It is visible only after the hemoglobin is partly or wholly removed from the corpuscle. In the embryo, where the corpuscles are so small, the nucleus is faintly visible in many corpuscles before the removal of the hemoglobin.

F. Rouleaux of the 142 mm. larva focused on the upper surface. In both *E.* and *F.* the corpuscles are shown of different sizes. Compare the maximum and minimum diameters in the table of measurements.

FIG. 43. (× about 1000). A single white blood-corpuscle in various amœboid phases, drawn freehand within two minutes.

FIG. 44. (× about 1000). Fibrin filaments of a larval lamprey. The filaments seem to radiate from centers, the centers appearing like white blood-corpuscles. Some of the filaments are moderately coarse, others exceedingly fine. *c.* a red blood-corpuscle with eccentric nucleus.

FIG. 45. (× about 1000). Human blood fibrin, to show the coarseness of the filaments and also centers of radiation. *c.* A red corpuscle drawn at the same scale.

FIG. 46. (× 700). Zoosperms of a lake lamprey. Three are shown entire. On each is a bulbous termination of the tail, and in the one at the right is an enlargement of the tail near the tip.

A. Two heads (× 2750). In the one at the right are shown two clear highly refractive bodies.

FIG. 47. Zoosperms of the sea lamprey. A single zoosperm drawn entire and magnified 700 diameters.

A. A head and the bulbous termination of the tail (× 2750.)

FIG. 48. Zoosperms of the brook lamprey. Two entire ones are shown at a magnification of 700. The tail of the one at the right is nearly uniform and ends in a point. The one at the left ends by a little knob as with the lake and sea lamprey.

A. Two heads magnified 2750 diameters.

FIG. 49. (Natural size). A glass vessel containing sand and water with a larval lamprey in its burrow, to show the position naturally assumed by the larvæ.

FIG. 50. (× 3). Head of a lake lamprey in the transforming stage to show the narrowed head and the snow white pineal eye.

1, 2. The first two branchiopores. *dc.* Posterior dorsal cartilage.

epi. Epiphysis or pineal eye surrounded by a light area.

n. Nostril with the opening directed obliquely cephalad

FIG. 51. Oblique view of the head and branchial region of an adult lamprey showing the direction of the expiratory currents from the branchiae and from the nasal sac.

bp. The branchiopores.

n. Nostril pointing obliquely cephalad.

so. Sensory organs, or nerve papillæ. Compare plates V and VI.

FIG. 52. (×4½). Frontal section, looking dorsad, of a larval lamprey, to show the velum and the course of the respired water.

1, 2, 3. Branchiopores covered with valves extending from the cephalic edge. *b*, *b*, *b*, *b*, Branchiae seen in section.

h. Hood or upper lip.

t. Oral tentacle. *v*, *v.* Velum. The two independent velar folds are shown in section.

vl. Valve over the branchiopore. In this one it is open for the passage of the expiratory stream, which is indicated as passing between the lamellæ of two contiguous gills.

The arrows show the stream entering the mouth through the straining tentacles, then between the two halves of the velum into the branchial chamber where it divides, part passing out between the gills of each side, and through the corresponding branchiopores.

FIG. 53, 54, 55. (×4½). Three views of the valves at the opening of the branchiopores that serve to direct the streams of water in inspiration and in expiration in the adult.

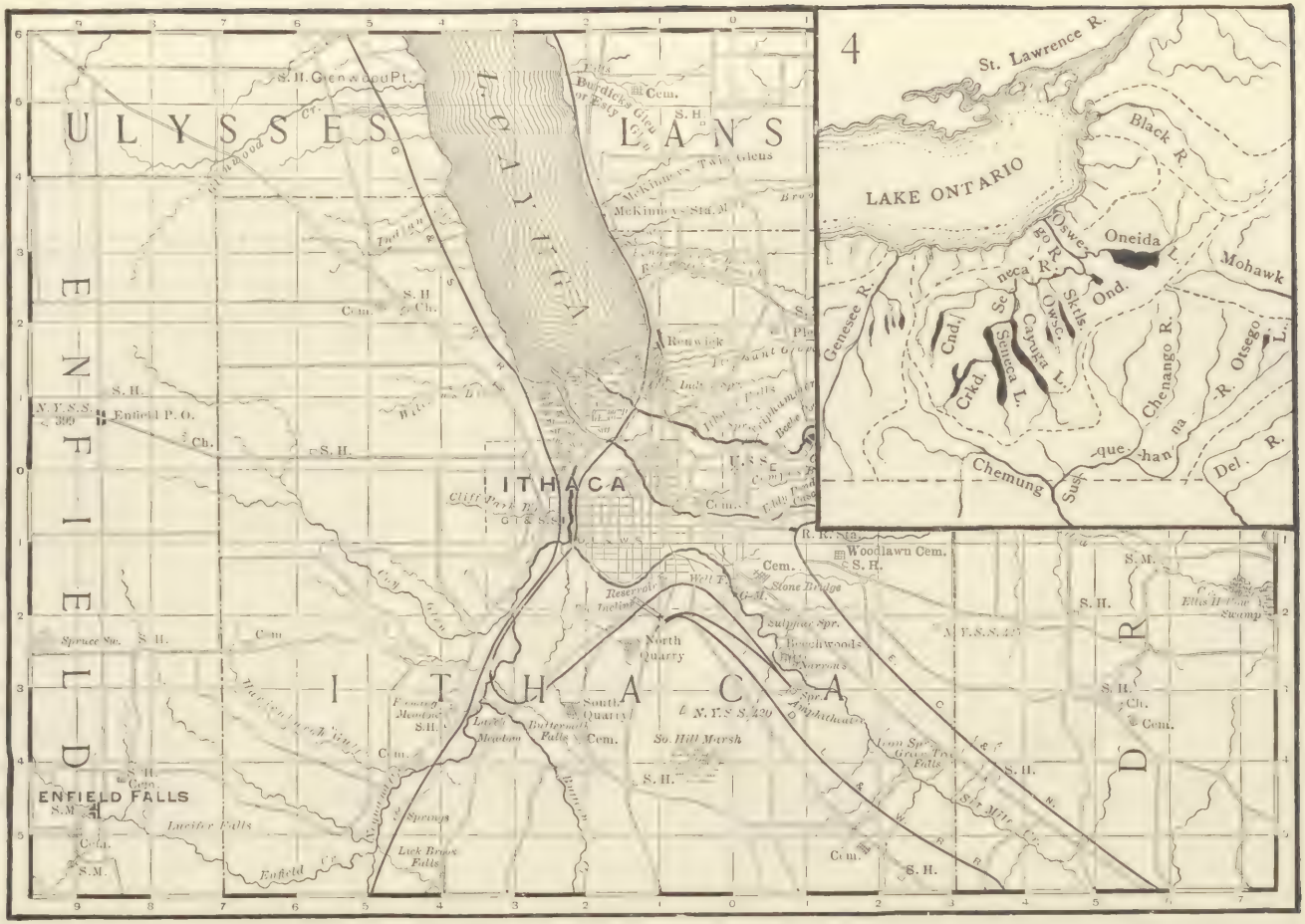
b, *b.* Branchiæ seen in section.

cl. Clavus or peg. A small, stiff, pointed body about 2 mm. high, arising on the caudal margin, and opposite the middle of the branchiopore. In expiration the two valves meet at this point, as shown in figure 55.

p. Fringe of papillæ on the caudal margin of the branchiopore. Their relation to the clavus is well shown in fig. 55.

vl. Valves. There are two, one extending dorso-ventrad as shown entire in fig. 55, and in section in fig. 53, 54. This one corresponds with the single valve of the larva.

The second, is a double valve within the branchiopore. In inspiration the two parts move up against the cephalic side of the branchiopore and are covered with the ectal or transverse valve and thus serve to guide the water directly into the gill sac. In expiration, fig. 54, 55, they rest against the caudal wall of the branchiopore, and, with the ectal transverse valve, make a tube directed obliquely caudad, thus giving a corresponding direction to the expiratory streams of water. See also fig. 51, 52.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Six Mile Creek
Enfield Creek
Lucifer Falls
Buttermilk Falls
Lick Brook Falls
Cliff Park
Renwick
McKinney's
Burdick's Glen or Estey Glen
Stone Bridge
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Beechwoods
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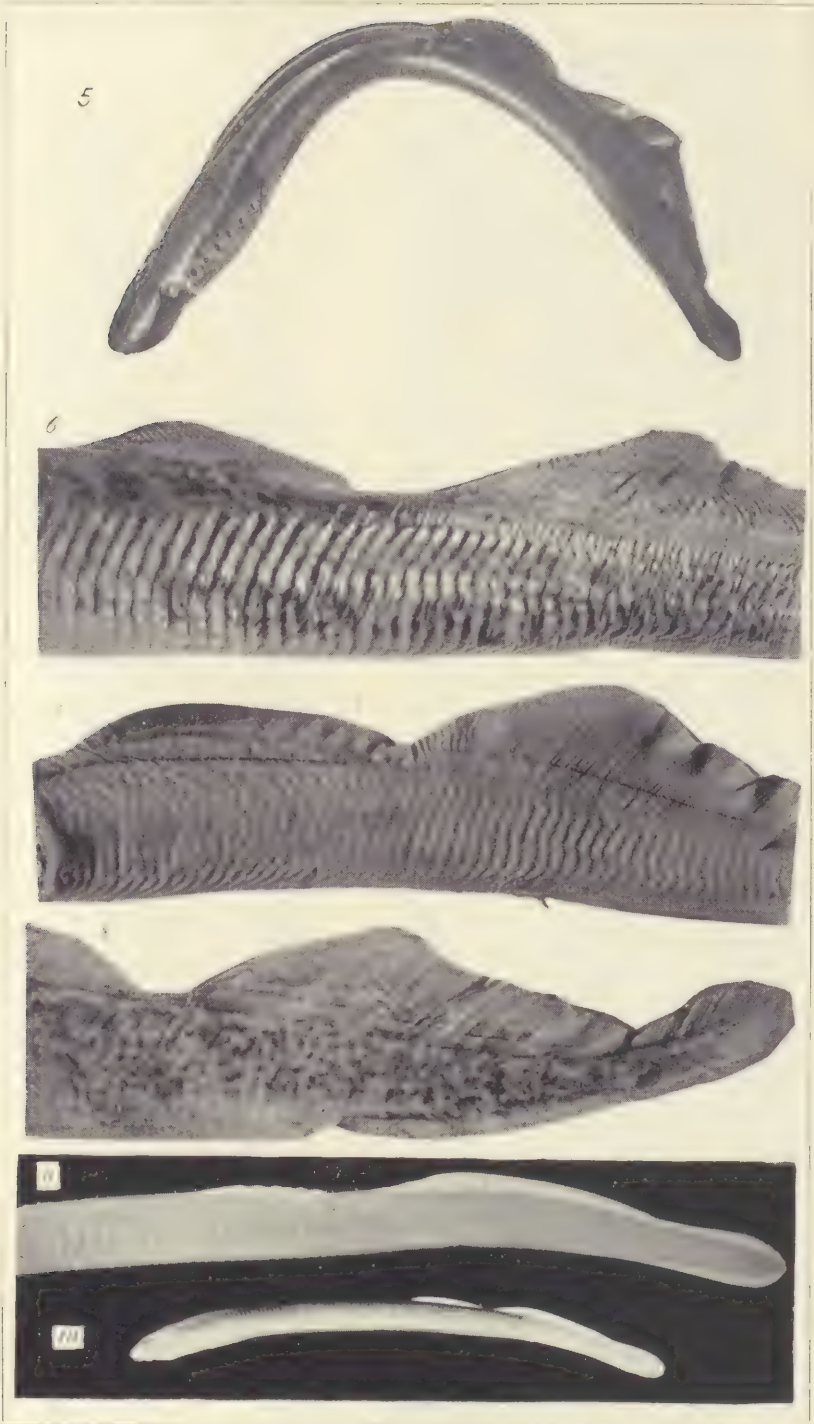
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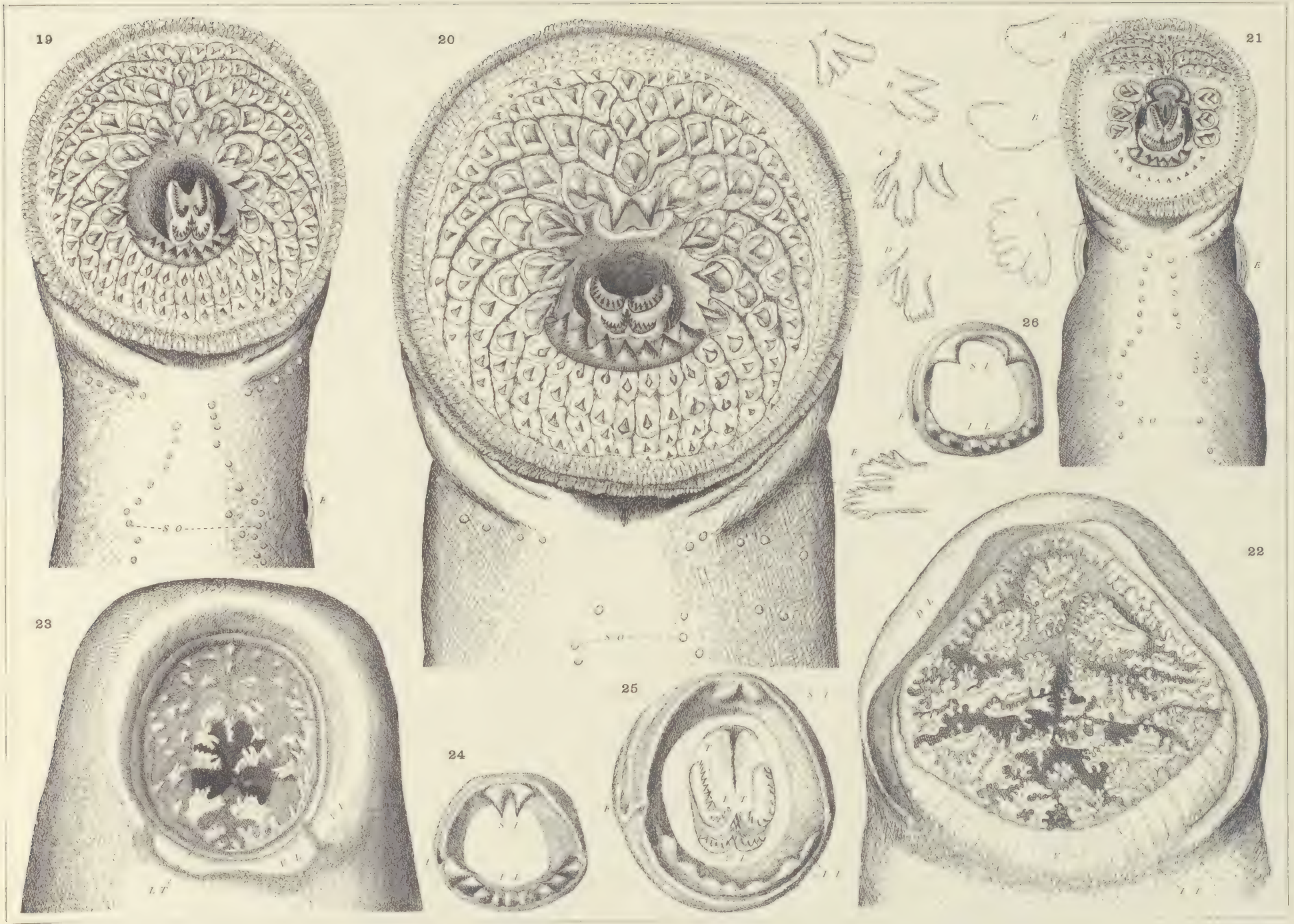
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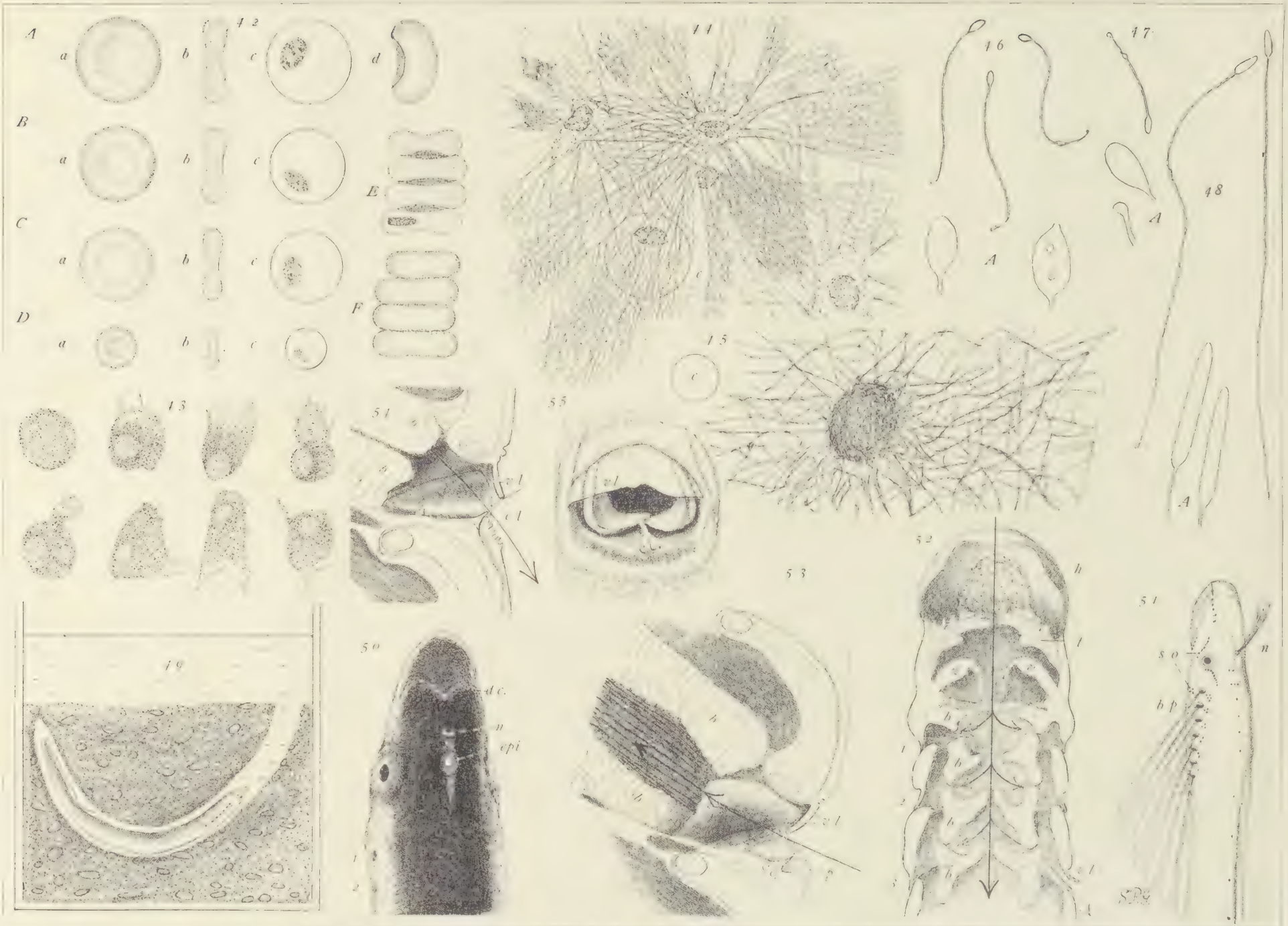
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